



Solar radiation and ENSO predict fruiting phenology patterns in a 15-year record from Kibale National Park, Uganda

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ABSTRACT

Fruiting, flowering, and leaf set patterns influence many aspects of tropical forest communities, but there are few long-term studies examining potential drivers of these patterns, particularly in Africa. We evaluated a 15-year dataset of tree phenology in Kibale National Park, Uganda, to identify abiotic predictors of fruit phenological patterns and discuss our findings in light of climate change. We quantified fruiting for 326 trees from 43 species and evaluated these patterns in relation to solar radiance, rainfall, and monthly temperature. We used time-lagged variables based on seasonality in linear regression models to assess the effect of abiotic variables on the proportion of fruiting trees. Annual fruiting varied over 3.8-fold, and inter-annual variation in fruiting is associated with the extent of fruiting in the peak period, not variation in time of fruit set. While temperature and rainfall showed positive effects on fruiting, solar radiance in the two-year period encompassing a given year and the previous year was the strongest predictor of fruiting. As solar irradiance was the strongest predictor of fruiting, the projected increase in rainfall associated with climate change, and coincident increase in cloud cover suggest that climate change will lead to a decrease in fruiting. ENSO in the prior 24-month period was also significantly associated with annual ripe fruit production, and ENSO is also affected by climate change. Predicting changes in phenology demands understanding inter-annual variation in fruit dynamics in light of potential abiotic drivers, patterns that will only emerge with long-term data.

Key words: climate change; ENSO; fruiting patterns; phenology; rainfall; solar radiation.

THE FRUITING, FLOWERING, AND LEAF SET PATTERNS OF TROPICAL forests can have significant effects on the fitness of trees that produce these patterns. For example, fruiting at the wrong time may result in seeds germinating under conditions that are unsuitable for establishment and survival (van Schaik *et al.* 1993, Curran & Webb 2000, Chapman *et al.* 2005). Changes in the timing of phenophase events can also have cascading effects and influence mutualistic interactions such as those between trees and the animals that both disperse seeds and are dependent on trees for food resources (Rafferty *et al.* 2015). For example, an evaluation of 12 years of data on chimpanzee reproduction and tree phenology in Kibale National Park, Uganda, demonstrated that the availability of fruit strongly influenced the reproductive performance in this endangered chimpanzee population (Wrangham *et al.* 1991, 1996, Thompson & Wrangham 2008). Thus, understanding patterns and drivers of fruiting, flowering, and leaf set

has important implications for forest communities and their potential response to climate change (Root *et al.* 2003, Pau *et al.* 2011, Rafferty *et al.* 2015).

Proposed drivers of phenological patterns of tropical rain forests include the following: rainfall, day length, irradiance, and temperature (Opler *et al.* 1976, Ashton *et al.* 1988, van Schaik *et al.* 1993, Newbery *et al.* 1998, but see Polansky & Boesch 2013); the El Niño Southern Oscillation (ENSO) Index (Chang-Yang *et al.* 2016); mode of seed dispersal (Smythe 1970, Wheelwright 1985); activity of pollinators or seed dispersers (Snow 1965, Frankie *et al.* 1974, Rathke & Lacey 1985); variation in germination conditions (Janzen 1967, Frankie *et al.* 1974); the potential to swamp the ability of seed predators to destroy seeds (Visser *et al.* 2011); life history traits (Davies & Ashton 1999, Pau *et al.* 2011); and relative abundance of the trees themselves (van Schaik *et al.* 1993). For example, a hypothesis that has received strong support for why some tree species exhibit mast fruiting (synchronous intermittent production of large seed crops in perennial plants) is that it is an adaptive reproductive trait that

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satiates seed predators, allowing more seedlings to establish (Janzen 1971, Kelly & Sork 2002).

Drivers of phenological patterns, both abiotic and biotic, are likely to be affected by climate change. Over the past century, global mean temperatures have risen significantly (0.85°C between 1880 to 2012) as has the rate of global warming (Root *et al.* 2003, IPCC 2014), and climate change scenarios predict an increase of at least 1.0 to 3.7°C between the reference period of 1986–2005 and 2081–2100 (Pau *et al.* 2013, IPCC 2014). The Intergovernmental Panel on Climate Change (IPCC) has identified Africa as one of the most vulnerable regions with respect to global climate variability and change, which may interact with existing problems of resource overexploitation, human population growth, and widespread poverty (IPCC 2014). Numerous documented shifts in the distribution, population abundance, and life history of species highlight the significance of climate change in altering species and community characteristics (Hannah *et al.* 2002, Parmesan & Yohe 2003, Chen *et al.* 2011). However, it is increasingly evident that ecological adjustments in response to climate change can occur in response to even slight shifts in temperature (van Vliet & Schwartz 2002, Walther *et al.* 2002). For example, the average first flowering date of 385 British plant species has advanced by 4.5 days over the past decade compared to the previous four decades (Fitter & Fitter 2002, see also Wolkovich *et al.* 2012).

Documenting ecological changes in plant and animal communities in response to climate change is critical to understanding and predicting regional and global phenological patterns, and to identifying the proximate driver(s) of change in the focal taxa. Phenological cycles of trees are complex, with many abiotic and biotic drivers, and cascading biotic consequences (van Schaik *et al.* 1993). Thus, identifying primary abiotic drivers of phenophase patterns may require long-term data on tree leaf and fruiting dynamics, as well as data on a number of proposed predictors. Such data are rare for tropical forests.

Here, we quantify seasonal and inter-annual phenological fruiting patterns of a community of tropical trees over 15 years in Kibale National Park, Uganda, and identify abiotic predictors of phenophase dynamics. We discuss the implications of our results for understanding and predicting effects of climate change on tropical forest communities.

METHODS

STUDY SITE.—The study was conducted in Kibale National Park, which is near the foothills of the Rwenzori Mountains in southwestern Uganda (795 km², 0°13'–0°41'N and 30°19'–30°32'E) (Chapman & Lambert 2000, Chapman *et al.* 2010a). The area is mid-altitude (1500 m) moist forest (Holdridge 1967), near the Makerere University Biological Field Station. The site (K-30 forestry compartment) has never been commercially harvested, but a few large stems (0.03 to 0.04 trees/ha) were removed by pit-sawyers before 1970 (Chapman *et al.* 1997, 2010a). In this equatorial region, rainfall is bimodal with two wet and two dry seasons each year and an annual average rainfall of 1680 mm

(1990–2015; Colin Chapman unpubl. data) (Stampone *et al.* 2011).

BIOTIC VARIABLES.—Here, we report on monthly phenological data collected from June 1998 to December 2013 (data could not be collected in June 2009 and June 2010). Phenological patterns were quantified using a trail system that monitored ~326 individual trees from 43 species (average number of individuals per species = 7.6, range = 1–13 individuals per species; Chapman *et al.* 1994). The trail covered an area of approximately 4 km². Only trees with a diameter at breast height (dbh) ≥10 cm and known to be of the size greater than the minimum fruiting size were included in the survey. The trees were selected to include major food trees of both the folivorous and frugivorous primates occurring in the area; however, as both fruit and leaf eating primates were of interest, they represent many of the common trees in the area (a description of the entire tree community can be found in Chapman *et al.* 1997, Struhsaker 1997, and Chapman *et al.* 2010a). The number of trees varied slightly among months due to mortality. In these cases, trees of the same species and dbh were added to the monitoring regime within two months.

We visually examined the crown of each tree from the ground to determine the presence of different leaf stages (*i.e.*, leaf buds, young leaves, and mature leaves), flowers, and unripe and ripe fruit. This was done once a month close to the middle of the month. We evaluated the relative abundance of fruit on a scale of 0–4, which proved to be consistent between observers (Struhsaker 1975, 1997, Chapman *et al.* 1994). For some tree species, there is no color change associated with ripening (*e.g.*, *Monodora myristica*; Balcomb & Chapman 2003), or the fruit may exhibit a color change before it has its highest nutritional value (Worman & Chapman 2005, Rothman *et al.* 2012). As a result, for each fleshy-fruited species, we defined fruit as ripe when they were first eaten by frugivores, and after they had reached full size, based on our experience (we have been monitoring the foraging behavior of the frugivorous primates since 1989; Chapman pers. obs.). For wind-dispersed species, we considered a tree to have mature fruit when dehiscent fruits opened and seeds could be found under the parent canopy.

ABIOTIC VARIABLES.—We collected data on rainfall and temperature at the field station using a standard weather station, and a large circular rain gauge. We calculated mean monthly rainfall, and mean monthly maximum and minimum temperatures.

We estimated solar radiation based on data acquired from the Satellite Application Facility on Climate Monitoring (CM SAF; Schulz *et al.* 2009, Antonanzas-Torres *et al.* 2014, Rodriguez-Galiano *et al.* 2016). To acquire average monthly incoming solar radiation at the level of the phenology trail, we used estimates for incoming short wave radiation at the surface of the earth. These data from CM SAF represent a satellite-based estimate of the solar surface irradiance using a modified version of the Heliosat algorithm (Posselt *et al.* 2012). When compared to ground control stations, the mean absolute bias between observed and predicted values using this approach was 7.99/

Wm^2 with a standard deviation of $8.1/\text{Wm}^2$, and a mean error of $4.40/\text{Wm}^2$ indicating an upwards bias (Posselt *et al.* 2012). To cover the same time period as the phenology data, we made use of two datasets, one from January 1998 to December 2005 at a spatial resolution of 0.03×0.03 decimal degrees (Posselt *et al.* 2011) and a second one from January 2006 to December 2013 at a spatial resolution of 0.05×0.05 decimal degrees (Müller *et al.* 2015). Given the different spatial resolutions of these datasets, we checked the agreement between the two datasets during an 8-year period in which they overlap, and found that they largely capture the same information (Pearson's $r = 0.97$, $\text{RMSE} = 2.11/\text{Wm}^2$). In cases where the phenology trail was found in more than one pixel, the average was used. This resulted in 192 estimates of average monthly solar radiation for the area covered by the phenology trail.

To capture the intensity of El Niño Southern Oscillation (ENSO), we also included the Multivariable ENSO Index (MEI) as a monthly time series. The MEI is a composite measure and is based on sea level pressure, zonal and meridional components of the surface wind, sea surface temperature, surface air temperature, and total cloudiness fraction of the sky (<https://www.esrl.noaa.gov/psd/enso/mei/>).

STATISTICAL ANALYSIS.—Across all observations, we measured the proportion of trees displaying any degree of fruiting (considering ripe fruit only) by assessing the proportion of plants with abundance scores greater than zero. We visualized the overall time series for our variable of primary interest: monthly proportion of fruiting plants, in addition to the abiotic drivers (solar irradiance, rainfall, ENSO, and average maximum and minimum temperature).

To quantify whether or not the phenology and abiotic patterns were cyclic, we conducted a spectral analysis on the monthly biotic and abiotic time series to obtain estimates of the power spectral density (Warner 1998). Peaks in the power spectral density correspond to the estimated periodicity in the underlying time series. If there are no peaks, then the underlying time series has no periodicity. For all spectral analyses, secular trends were first removed from each monthly time series using a LOESS filter with smoothing parameter of 0.33. Then, nonparametric estimates of the power spectral density were obtained using a discrete Fourier transform. The raw periodogram was smoothed using a Daniell filter (a type of moving average). Preliminary analyses demonstrated that fruiting in Kibale displays a distinct annual seasonality; thus, a fruiting year was defined as the 12-month period from June through May, which is centered on December and January: the months of highest annual fruiting. We examined the onset of the fruiting season by examining the proportion of total annual fruiting that occurred in the first five months of each fruiting season.

To identify drivers of annual fruiting, we (1) removed the seasonal component from each abiotic variable (except MEI, as this index is already standardized and without seasonality) using the residuals from a linear model with a categorical variable corresponding to month of the year; (2) measured the monthly

lagged mean of each of the abiotic variables for both a 12-month retrospective window and a 24-month retrospective window; and then (3) averaged the monthly values of these measures over the fruiting year. We used these lagged annual abiotic variables as predictors in linear regression models with annual proportion of fruiting (% of trees bearing ripe fruit) as the dependent variable. To control for autocorrelation between years, we used a generalized least squares model that accounted for AR(1) correlation. For each of the bivariable models, we only included the single lagged covariate. To improve prediction and adjust estimated effect sizes for dependencies between the abiotic variables, we built two multivariable models that included all five abiotic variables (one using the 12-month lagged abiotic variables and the other using the 24-month lagged abiotic variables).

To identify drivers of monthly fruiting, we conducted analogous bivariable and multivariable analyses using the monthly level time series. The dependent variable was the mean of the monthly proportion of ripe fruit, and the five abiotic variables represented the lagged mean over 12- and 24-month retrospective periods. All models included month of the year as a categorical variable to capture regular intra-annual variation.

For all multivariable models, variance inflation factors were calculated to assess the presence of multicollinearity. Initial VIF estimates revealed the presence of high levels of multicollinearity for several variables in each of the multivariable models. To address this, minimum temperature was not included in any of the final multivariable models due to its strong relationship with maximum temperature. All variables in each model had low VIFs (<2) after minimum temperature was removed.

RESULTS

Across 185 months, an average of 278 trees were observed in each month (range = 226–300). The median proportion of fruiting trees was 7.4% (range = 3.3–13.3; Fig. 1). Median monthly average rainfall was 3.3 mm per day (range = 0.17–8.5; Appendix S1). Mean solar irradiance was $209/\text{Wm}^2$ (range = 165–265). Monthly minimum temperature averaged 14.5°C (range = 12.5–16.9) and maximum temperature averaged 25.6°C (range = 24.0–29.9).

SPECTRAL ANALYSIS.—We conducted a spectral analysis to quantify whether or not the phenology and abiotic patterns were cyclic (Appendix S2). This analysis of the monthly fruiting data demonstrated a distinct peak in spectral power at frequencies that corresponded to annual periodicity (frequency = $1/12$; Appendix S1). As expected, rain, minimum temperature, maximum temperature, and solar radiation displayed spectral power peaks at frequencies that corresponded to annual (frequency = $1/12$) and biannual (frequency = $1/6$) periodicities; however, all subsequent analyses were conducted using annual data, as our response variable (fruiting) showed a clear annual peak.

INTRA-ANNUAL PATTERNS.—Fruiting was highest in the October-to-January period (Fig. 2), peaking in December (mean = 11.4%).

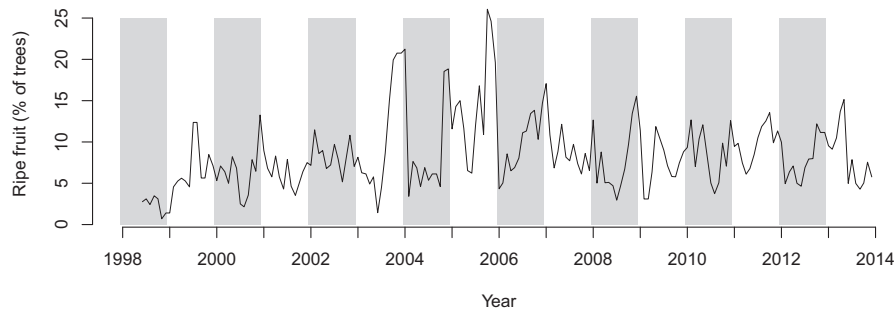


FIGURE 1. The monthly fruiting of trees on the phenology trail monitored in Kibale National Park, Uganda, over 15 years. The gray bar pattern signifies subsequent years and allows an easier evaluation of pattern.

Abiotic variables exhibited the peaks as illustrated in the spectral analysis (Appendix S2). When average fruiting was plotted across the 12 months of the year, fruiting was highest in the October-to-January period (Fig. 2), peaking in December (at 11.4%).

INTER-ANNUAL PATTERNS.—The data included 15 complete years of fruiting data. Annual fruiting varied over a 3.8-fold range (range = 3.3–12.3%, coefficient of variation [CV] = 28%). For solar radiation and temperature, inter-annual variation was very small (solar radiation range = 201.9–218.1, CV = 2%; daily average maximum temperature range = 23.9–26.7, CV = 3%; daily average minimum temperature range = 13.8–16.2, CV = 4%). Inter-annual variation in rainfall fell between that of fruiting and that of the other abiotic variables (range = 2.4–4.0, CV = 12%).

Variation in the magnitude of annual fruiting was not associated with earlier arrival of the fruiting period, but was associated with the proportion of fruiting occurring in the peak fruiting period. In general, years with an abundance of fruit distinguished themselves from the years where fruit was relatively scarce only in the peak fruiting period (Fig. 3).

Bivariable analyses of annual fruiting were based on 13 years of data because 2 years of retrospective data were used to measure abiotic predictor variables. In these analyses (Table 1, Fig. 4), solar irradiance and ENSO in the prior 24-month period were the only predictors significantly associated with increased annual ripe fruit production (4.1% increase in ripe fruit production per 10-pt increase in solar irradiance, 95% CI = 1.2–7.0; 2.7% increase per 1-pt increase in ENSO, 95% CI = 0.3–5.0). To help explain how the ENSO influenced fruit production, we conducted an analysis of time-series cross-correlation between local climatic variables and ENSO (Fig. 5). Multivariable analyses suggested that the 24-month lag model yielded better prediction of ripe fruit production as compared to all the bivariable models and the 12-month multivariable model. In the 24-month multivariable model, solar irradiance and ENSO were the variables most strongly associated with ripe fruit production.

Bivariable analyses of monthly fruiting yielded similar results (Table 2), although associations for solar irradiance did not reach the threshold of statistical significance (2.7% increase in ripe fruit production per 10-pt increase in solar irradiance, 95% CI = –1.9 to 7.3; 3.2% increase per 1-pt increase in ENSO, 95%

CI = 0.7–5.7). In the 24-month multivariable model, solar irradiance and ENSO were the variables most strongly associated with ripe fruit production, after adjusting for regular monthly seasonality.

DISCUSSION

Solar irradiance and ENSO were the strongest predictors of fruiting in Kibale National Park, Uganda. Solar irradiance may reflect the availability of sufficient energy to invest in fruit, which can affect both inter- and intra-annual patterns. Inter-annual variance in cloud cover may lead to variation in fruiting because in cloudy years, trees may need a longer time to meet the solar radiation requirements required for fruit ripening. Previous studies suggest that solar irradiance is a determinant of leaf and flower flush and that plants synchronize these phenophases with periods of the greatest assimilation potential and the least damage to leaves from herbivores (van Schaik *et al.* 1993, Wright & Van Schaik 1994, Parmesan & Hanley 2015). For example, considering a 30-year record of flowering, Wright and Calderón (2018) demonstrated that irradiance predicted flowering times well for 10 species. With respect to fruiting, Wright and Calderón (2006) demonstrated a connection between the peaks and troughs of fruit production to changes in cloud cover and solar irradiance. Furthermore, an experimental study that augmented the light available to *Luebea seemannii* canopy trees during cloudy periods resulted in a significant increase in reproduction (Graham *et al.* 2003), which suggests that light levels limit sun-exposed canopy trees. Our findings, in combination with these previous studies, highlight the importance of solar radiation to trees in timing their overall phenophases. Other factors likely also play a role. For instance, by fruiting in December in Kibale, dispersed seeds have the potential to germinate and establish at the start of the second, less intense, wet season in March–April. In addition, if fruits are on the tree when solar irradiance is high, fruit ripening may be accelerated (Smart *et al.* 1988), resulting in a decrease in the amount of time seeds are susceptible to predators prior to dispersal.

It is likely that solar irradiance is strongly influenced by cloud cover, which will be altered if climate change results in either wetter or drier conditions. Results from the General Circulation Model simulations by the IPCC (2014) show that East

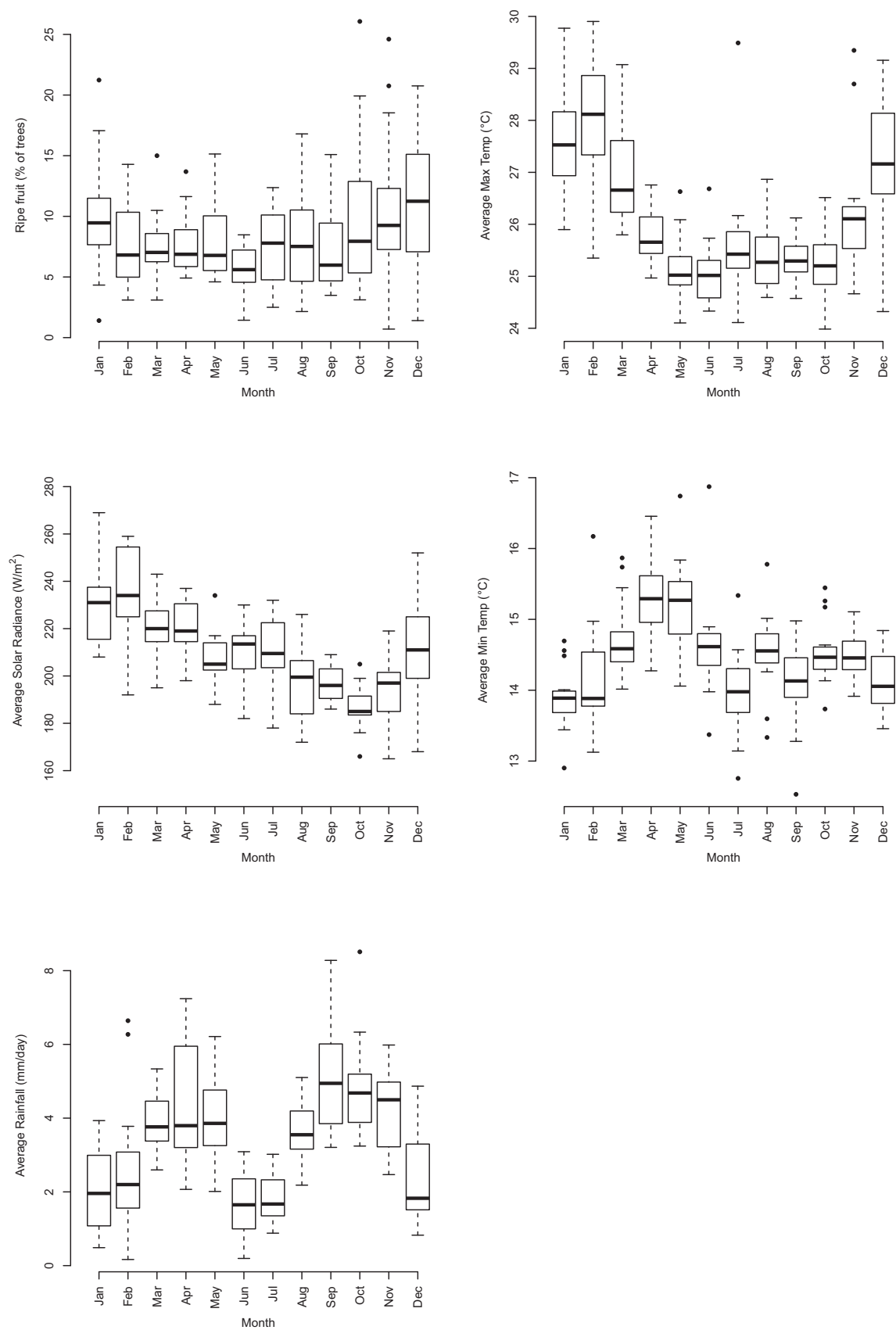


FIGURE 2. Average monthly fruiting, solar irradiance, rainfall, maximum temperature, and minimum temperature, Kibale, Uganda, 1996 to 2013.

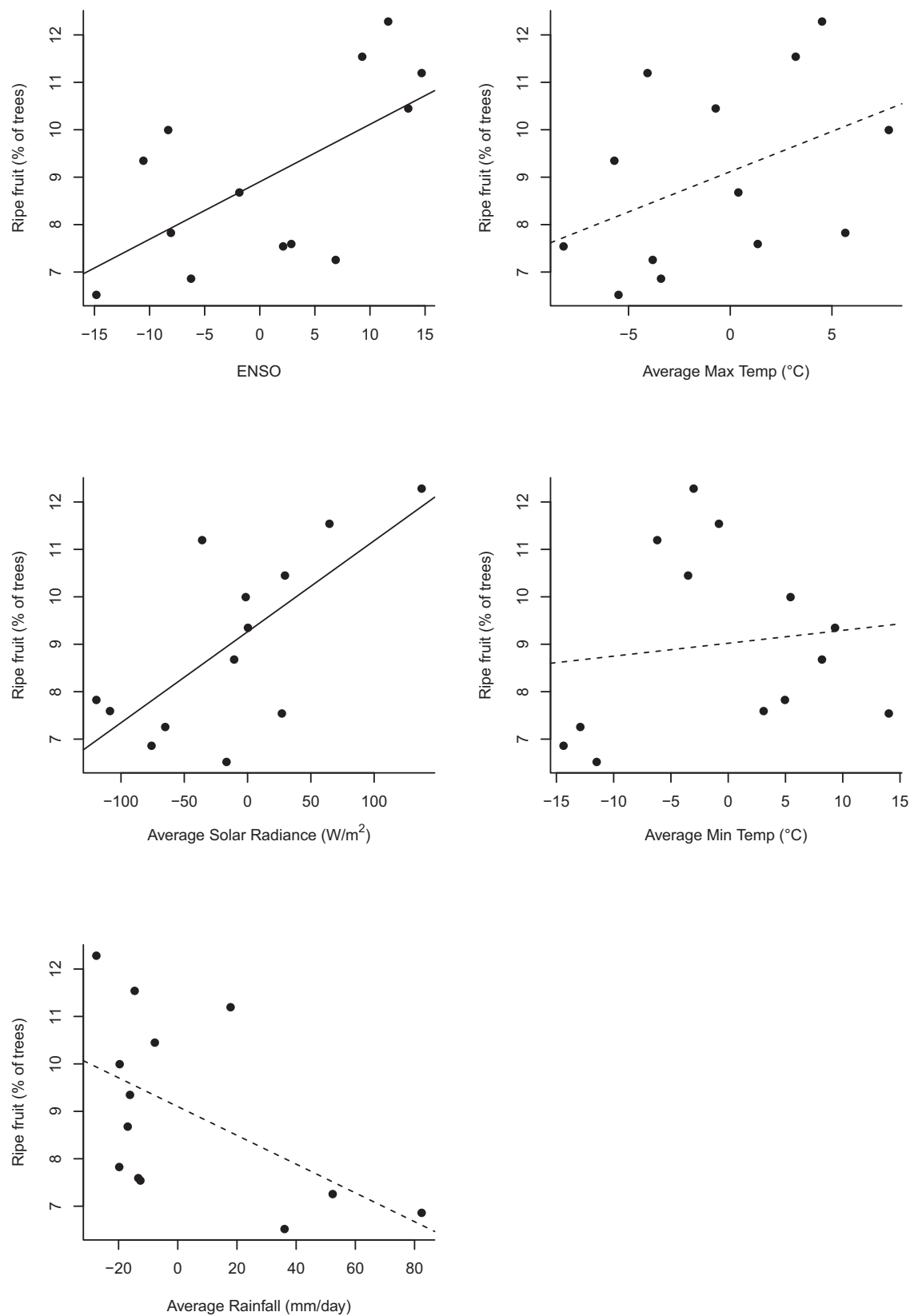


FIGURE 4. Annual fruiting as a function of abiotic predictors in the 2-year period encompassing the concurrent and prior fruiting years. Lines represent the fitted linear regression estimates (solid, $P < 0.05$; dashed, $P > 0.05$).

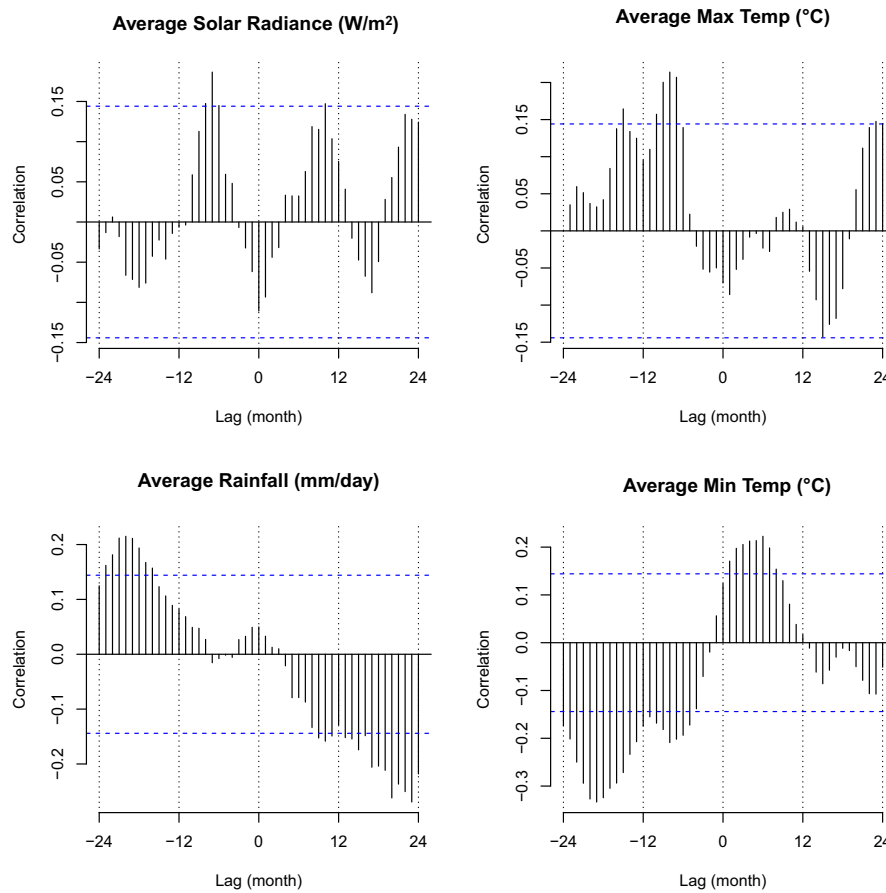


FIGURE 5. An analysis of time-series cross-correlation between local climatic variables and ENSO, which illustrates interaction between variables.

example, we found an increase in fruiting was associated with positive ENSO values (El Niño phase) on the one hand, which seems to contradict the positive relationship between fruiting and irradiance on the other hand (*i.e.*, if El Niño years have more rainfall in this area of the Albertine Rift and consequently less irradiance, why is ENSO related to increasing fruit production?). However, considering the lags helps clarifying this apparent contradiction. We documented that an increased MEI was associated with higher-than-normal levels of solar irradiance 6 months in the past, followed by lower-than-normal solar irradiance (and higher-than-normal rain) in the present. The fact that there is variation in the onset of the rains in each season and that the first rainy season in a year typically has less rain than the second likely introduces variance into the system. Regions with two rainy seasons may differ from those with one, and the effect of local features calls for the collection and analysis of more long-term phenology data. Areas with two rainy season patterns, like East Africa and the Western Ghats, may provide variation in potential drivers that are useful in teasing apart the effects of different abiotic factors.

Many tropical mammals and birds rely heavily on dietary fruit (Howe & Smallwood 1982, Richards 1996, Janson & Chapman 1999), and fruit availability has been shown to be an

important selective force influencing anatomy, grouping patterns, ranging, population abundance, and even patterns of extinction in frugivore species (Chapman *et al.* 1995, 2010b, Marshall *et al.* 2009). Our evaluation of the availability of fruit in Kibale revealed distinct periods of fruit abundance, as well as periods of acute scarcity, often lasting a number of months. Such periods likely have important downstream effects on animal communities. Periods of peak fruit availability and variation in inter-annual fruiting intensity during peak fruiting may be particularly important for animal species that synchronize reproduction with fruit availability (Thompson & Wrangham 2008). Our analysis quantifies community level patterns, but all fruiting tree species may not respond the same, in fact it is likely that they will not. If this is the case, deciphering and predicting how specific frugivores' responses will be affected by climate change will be difficult because the relative role of tree species in the foraging ecology and population dynamics is known to vary, but this has rarely been quantified (Shanahan *et al.* 2001, Rode *et al.* 2006, Hanya & Chapman 2013).

Plant fruiting dynamics are not just influenced by abiotic factors; animals play significant roles on both ecological and evolutionary timescales. The coefficients of variation of our response variable, proportion of individuals fruiting, were much higher

TABLE 2. Predictors of increased monthly percentage of trees with ripe fruit as a function of abiotic factors (monthly analysis).

Abiotic predictor	Bivariable models				Multivariable models			
	1-year lag		2-year lag		1-year lag		2-year lag	
	% Change (95% CI)	AIC (Δ)	R ² (%)	% Change (95% CI)	AIC (Δ)	R ² (%)	% Change (95% CI)	AIC (Δ)
ENSO Index	1.7 (−0.3, 3.7)	825.6 (0)	24.9	3.2 (0.7, 5.7)	822.3 (0)	30.1	2.9 (0.5, 5.3)	824.6 (−2.0)
Average solar irradiance	1.4 (−0.9, 3.6)	827.1 (1.5)	24.7	2.7 (−1.9, 7.3)	827.1 (4.8)	24.7	1.4 (−2.0, 4.7)	
(per 10-point increase)								
Average rainfall (cm/day)	−4.3 (−11.2, 2.6)	826.9 (1.3)	23.9	−5.4 (−13.7, 2.9)	826.7 (4.4)	24.0	−1.6 (−10.0, 6.8)	
Average max temp. (°C)	1.5 (−1.5, 4.6)	827.3 (1.7)	21.8	3.4 (−1.4, 8.2)	826.3 (4.0)	22.2	2.6 (−2.0, 7.1)	
Average min temp. (°C)	1.1 (−2.0, 4.1)	827.9 (2.3)	20.8	1.1 (−2.3, 4.5)	827.9 (5.6)	20.9	NA	NA

AIC: Akaike's Information Criterion; Δ : AIC difference relative to best model (bivariable models) or null model (multivariable models, AIC = 55.6). Negative values represent improved model fit; CI: confidence interval.

R²: The goodness of fit was calculated as the proportion of the total variance explained by the model.

ENSO Index—per 1-point increase.

[†]Adjusted for autocorrelation using generalized least squares

than those of the abiotic covariates. Some of the variation in fruiting will be caused by biotic events occurring to the trees prior to them fruiting. Folivores have the capability of literally defoliating large tropical trees, to the extent that with repeat visits they can lead to a trees death (Chapman *et al.* 2013a, Myers & Sarfraz 2017). Such events could result in a tree receiving insufficient energy to fruit or only producing a reduced fruit crop. Similarly, folivores often feed heavily on flowers, effectively eliminating pollination and stopping fruit set. Within Kibale, red colobus monkeys (*Ptilocolobus tephrosceles*) feed so heavily on the flowers of *Markhamia lutea* that trees in the forest have not set fruit in decades, but trees in neighboring forest patches, without the colobus monkeys, fruit annually (Chapman *et al.* 2013b). Similarly, folivores can eat the unripe fruit of some species dramatically affecting fruiting (DaSilva 1992). In such cases, to understand how the dynamics of a trees fruiting is affected by climate change, studies will have to be conducted on the suite of pollinators/folivores/trees. In these cases, the process leading to ecosystem change is in the order of climate then animal then plant, rather than climate then plant then animal.

All the abiotic factors examined cycle together; thus, it is hard to confirm the effects of the individual factors unless all are measured at the same time providing an opportunity to parse out the effects of individual drivers. For instance, rainfall is inversely related to solar irradiance, and both interact with temperature. This likely explains many discrepancies in the literature with respect to factors driving phenological patterns. For example, we previously reported that minimum temperature in the previous dry season correlated with the number of trees that fruit in Kibale (see also Struhsaker 1997, Chapman *et al.* 1999). We proposed that as periods with low nighttime temperatures tend to be those with little insulating cloud cover and high levels of irradiance, this may permit the buildup of assimilates needed for fruiting. We went on to suggest that high irradiance promotes fruiting, a relationship supported by the current study. In a subsequent publication (Chapman *et al.* 2005), we showed that relationships between rainfall and fruiting were variable among four geographically separated sites in Uganda. This series of studies on phenophase dynamics in Ugandan forests highlights the importance of long-term (≥ 10 years) data sets and the need to simultaneously measure a suite of potentially important variables that could influence the timing and intensity of phenological events to facilitate statistical approaches that can reveal the most significant predictor variables. With data for some of these variables becoming available from satellite, this becomes more feasible for future studies and those that have existing data on plant phenological patterns. Specifically, the growing infrastructure of meteorological satellites has increased the availability of solar radiation estimates and ENSO data. This has resulted in increased coverage and spatial-temporal resolution at which solar radiation can be estimated (Harries *et al.* 2005, Schulz *et al.* 2009, Zhang *et al.* 2014). Furthermore, the relations we documented between ENSO and the proportion of fruiting trees were generally higher than those between local climatic variables and fruit production. This supports the claim that large-scale seasonal indices of

climate spanning several months or longer can outperform local climatic factors in explaining important ecological variable such as population dynamics and variation in demographic rates (Hallett *et al.* 2004, Stenseth & Mysterud 2005, Dunham *et al.* 2011). Thus, because of the importance of ENSO in our research, we suggest that researchers explore the predictive power of these large-scale climate indices.

In summary, regression modeling of annual fruiting revealed solar irradiance and ENSO as the strongest predictors of fruiting in Kibale National Park, Uganda. The projected changes in rainfall associated with climate change, and coincident variation in cloud cover suggest that fruiting dynamics may be affected by climate change. Predicting the nature of the response by the plant and animal community demands a better understanding of inter-annual variation in fruit dynamics in light of potential abiotic drivers and a much-improved understanding of the relative role of different fruiting trees to specific frugivores: patterns that will only emerge with long-term (>10 years) datasets.

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DATA AVAILABILITY

Data available at DOI = <https://doi.org/10.5281/zenodo.1194838>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

APPENDIX S1. Spectral analysis of the monthly fruiting of trees on the phenology trail monitored in Kibale National Park, Uganda, over 15 years.

APPENDIX S2. Monthly variation in climatic variable and % of trees monitored with ripe fruit in Kibale National Park, Uganda, over the duration of the study.

LITERATURE CITED

- ANTONANZAS-TORRES, F., F. J. MARTINEZ-DE-PISON, J. ANTONANZAS, AND O. PERPINAN. 2014. Downscaling of global solar irradiation in complex areas in R. J. Renew. Sustain. Energy 6: 063105.
- ASHTON, P. S., T. GIVINISH, AND S. APPANAH. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. Am. Nat. 132: 44–66.
- BALCOMB, S. R., AND C. A. CHAPMAN. 2003. Bridging the gap: Influence of seed deposition on seedling recruitment in a primate-tree interaction. Ecol. Monogr. 73: 625–642.
- CHANG-YANG, C. H., I. F. SUN, C. H. TSAI, C. L. LU, AND C. F. HSIEH. 2016. ENSO and frost codetermine decade-long temporal variation in flower and seed production in a subtropical rain forest. J. Ecol. 104: 44–54.
- CHAPMAN, C. A., T. R. BONNELL, J. F. GOGARTEN, J. E. LAMBERT, P. A. OMEJA, D. TWINOMUGISHA, M. D. WASSERMAN, AND J. M. ROTHMAN. 2013a. Primates as ecosystem engineers. Int. J. Primatol. 34: 1–14.
- CHAPMAN, C. A., T. R. BONNELL, R. SENGUPTA, T. L. GOLDBERG, AND J. M. ROTHMAN. 2013b. Is *Markhamia lutea*'s abundance determined by animal foraging? For. Ecol. Manage. 308: 62–66.
- CHAPMAN, C. A., L. J. CHAPMAN, A. L. JACOB, J. M. ROTHMAN, P. A. OMEJA, R. REYNA-HURTADO, J. HARTTER, AND M. J. LAWES. 2010a. Tropical tree community shifts: implications for wildlife conservation. Biol. Conserv. 143: 366–374.
- CHAPMAN, C. A., L. J. CHAPMAN, T. T. STRUHSACKER, A. E. ZANNE, C. J. CLARK, AND J. R. POULSEN. 2005. A long-term evaluation of fruiting phenology: importance of climate change. J. Trop. Ecol. 21: 31–45.
- CHAPMAN, C. A., L. J. CHAPMAN, R. W. WRANGHAM, G. ISABIRYE-BASUTA, AND K. BEN-DAVID. 1997. Spatial and temporal variability in the structure of a tropical forest. Afr. J. Ecol. 35: 287–302.
- CHAPMAN, C. A., AND J. E. LAMBERT. 2000. Habitat alteration and the conservation of African primates: Case study of Kibale National Park, Uganda. Am. J. Primatol. 50: 169–185.
- CHAPMAN, C. A., T. T. STRUHSACKER, J. P. SKORUPA, T. V. SNAITH, AND J. M. ROTHMAN. 2010b. Understanding long-term primate community dynamics: Implications of forest change. Ecol. Appl. 20: 179–191.
- CHAPMAN, C. A., R. W. WRANGHAM, AND L. J. CHAPMAN. 1994. Indices of habitat-wide fruit abundance in tropical forest. Biotropica 26: 160–171.
- CHAPMAN, C. A., R. W. WRANGHAM, AND L. J. CHAPMAN. 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. Behav. Ecol. Sociobiol. 36: 59–70.
- CHAPMAN, C. A., R. W. WRANGHAM, L. J. CHAPMAN, D. K. KENNARD, AND A. E. ZANNE. 1999. Fruit and flower phenology at two sites in Kibale National Park, Uganda. J. Trop. Ecol. 15: 189–211.
- CHEN, I.-C., J. K. HILL, R. OHLEMÜLLER, D. B. ROY, AND C. D. THOMAS. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333: 1024–1026.
- CURRAN, L. M., AND C. O. WEBB. 2000. Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipterocarpaceae. Ecol. Monogr. 70: 129–148.
- DASILVA, G. L. 1992. The western black and white colobus as a low energy strategist: activity budget, energy expenditure and energy intake. J. Anim. Ecol. 61: 79–91.
- DAVIES, S. J., AND P. S. ASHTON. 1999. Phenology and fecundity in 11 sympatric pioneer species of *Macaranga* (Euphorbiaceae) in Borneo. Am. J. Bot. 86: 1786–1795.
- DUNHAM, A. E., E. M. ERHART, AND P. C. WRIGHT. 2011. Global climate cycles and cyclones: consequences for rainfall patterns and lemur reproduction in southeastern Madagascar. Global Change Biol. 17: 219–227.
- FITTER, A., AND R. FITTER. 2002. Rapid changes in flowering time in British plants. Science 296: 1689–1691.
- FRANKIE, G. W., H. G. BAKER, AND P. A. OPLER. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. J. Ecol. 62: 881–919.
- GRAHAM, E. A., S. S. MULKEY, K. KITAJIMA, N. G. PHILLIPS, AND S. J. WRIGHT. 2003. Cloud cover limits net CO₂ uptake and growth of a rainforest tree during tropical rainy seasons. Proc. Natl. Acad. Sci. USA 100: 572–576.
- HALLETT, T., T. COULSON, J. PILKINGTON, T. CLUTTON-BROCK, J. PEMBERTON, AND B. GRENFELL. 2004. Why large-scale climate indices seem to predict ecological processes better than local weather. Nature 430: 71–75.

- HANNAH, L., G. F. MIDGLEY, T. LOVEJOY, W. J. BOND, M. BUSH, J. C. LOVETT, D. SCOTT, AND F. L. WOODWARDS. 2002. Conservation of biodiversity in a changing climate. *Conserv. Biol.* 16: 264–268.
- HANYA, G., AND C. A. CHAPMAN. 2013. Linking feeding ecology and population abundance: a review of food resource limitation on primates. *Ecol. Res.* 28: 183–190.
- HARRIES, J. E., J. E. RUSSELL, J. A. HANAFIN, H. BRINDLEY, J. FUTYAN, J. RUFUS, S. KELLOCK, G. MATTHEWS, R. WRIGLEY, A. LAST, J. MUELLER, R. MOS-SAVATI, J. ASHMALL, E. SAWYER, D. PARKER, M. CALDWELL, P. M. ALLAN, A. SMITH, M. J. BATES, B. COAN, B. C. STEWART, D. R. LEPINE, L. A. CORNWALL, D. R. CORNEY, M. J. RICKETTS, D. DRUMMOND, D. SMART, R. CUTLER, S. DEWITTE, N. CLERBAUX, L. GONZALEZ, A. IPE, C. BERTRAND, A. JOUKOFF, D. CROMMELYNCK, N. NELMS, D. T. LLEWELLYN-JONES, G. BUTCHER, G. L. SMITH, Z. P. SZEWczyk, P. E. MLYNCZAK, A. SLINGO, R. P. ALLAN, AND M. A. RINGER. 2005. The geostationary earth radiation budget project. *Bull. Am. Meteorol. Soc.* 86: 945–960.
- HOLDRIDGE, L. R. 1967. Life zone ecology. Tropical Science Center, San Jose Costa Rica, 206 pp.
- HOWE, H. F., AND J. H. SMALLWOOD. 1982. Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* 13: 201–228.
- IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Core Writing Team, R. K. Pachauri, and L. A. Meyer (Eds.). IPCC, Geneva, Switzerland.
- JANSON, C. H., AND C. A. CHAPMAN. 1999. Resources and the determination of primate community structure. *In* J. G. Fleagle, C. H. Janson, and K. E. Reed (Eds.). *Primate communities*, pp. 237–267. Cambridge University Press, Cambridge, UK.
- JANZEN, D. H. 1967. Synchronization of sexual reproduction of trees within a dry season in Central America. *Evolution* 21: 620–637.
- JANZEN, D. H. 1971. Seed predation by animals. *Annu. Rev. Ecol. Syst.* 2: 465–492.
- KELLY, D., AND V. L. SORK. 2002. Mast seeding in perennial plants: why, how, where? *Annu. Rev. Ecol. Syst.* 33: 427–447.
- MARSHALL, A. J., C. M. BOYKO, K. L. FEILEN, R. H. BOYKO, AND M. LEIGHTON. 2009. Defining fallback foods and assessing their importance in primate ecology and evolution. *Am. J. Phys. Anthropol.* in press 140: 603–614.
- MÜLLER, R., U. PFEIFROTH, C. TRÄGER-CHATTERJEE, R. CREMER, J. TRENTMANN, AND R. HOLLMANN. 2015. Surface solar radiation data set - heliosat (SARAH). 7: 8067–8101.
- MYERS, J. H., AND R. M. SARFRAZ. 2017. Impacts of insect herbivores on plant populations. *Annu. Rev. Entomol.* 62: 207–230.
- NEWBERY, D. M., N. C. SONGWE, AND G. B. CHUYONG. 1998. Phenology and dynamics of an African rainforest at Korup, Cameroon. *In* D. M. Newbery, H. H. T. Pins, and N. D. Brown (Eds.). *Dynamics of tropical communities*, pp. 267–607. Blackwell, Oxford, UK.
- OPLER, P. A., G. W. FRANKIE, AND H. G. BAKER. 1976. Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. *J. Biogeogr.* 3: 231–236.
- PARMESAN, C., AND M. E. HANLEY. 2015. Plants and climate change: complexities and surprises. *Ann. Bot.* 116: 849–864.
- PARMESAN, C., AND G. A. YOHE. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.
- PAU, S., E. M. WOLKOVICH, B. I. COOK, T. J. DAVIES, N. J. B. KRAFT, K. BOLMGREN, J. L. BETANCOURT, AND E. E. CLELAND. 2011. Predicting phenology by integrating ecology, evolution, and climate science. *Global Change Biol.* 17: 3633–3646.
- PAU, S., E. M. WOLKOVICH, B. I. COOK, C. J. NYTCH, J. REGETZ, J. K. ZIMMERMAN, AND S. J. WRIGHT. 2013. Clouds and temperature drive dynamic changes in tropical flower production. *Nat. Clim. Chang.* 3: 838–842.
- POLANSKY, L., AND C. BOESCH. 2013. Long-term changes in fruit phenology in a West African lowland tropical rain forest are not explained by rainfall. *Biotropica* 45: 434–440.
- POSSELT, R., R. W. MUELLER, R. STÖCKLI, AND J. TRENTMANN. 2012. Remote sensing of solar surface radiation for climate monitoring — the CM-SAF retrieval in international comparison. *Remote Sens. Environ.* 118: 186–198.
- POSSELT, R., R. MÜLLER, R. STÖCKLI, AND J. TRENTMANN. 2011. CM SAF Surface Radiation MVIRI Data Set 1.0 - Monthly Means / Daily Means / Hourly Means. S. A. F. o. C. Monitoring, editor.
- RAFFERTY, N. E., P. J. CARADONNA, AND J. L. BRONSTEIN. 2015. Phenological shifts and the fate of mutualisms. *Oikos* 124: 14–21.
- RATHKE, B., AND E. P. LACEY. 1985. Phenological patterns of terrestrial plants. *Annu. Rev. Ecol. Syst.* 16: 179–214.
- RICHARDS, P. W. 1996. The tropical rain forest. Cambridge University Press, Cambridge, UK.
- RODE, K. D., C. A. CHAPMAN, L. R. McDOWELL, AND C. STICKLER. 2006. Nutritional correlates of population density across habitats and logging intensities in redtail monkeys (*Cercopithecus ascanius*). *Biotropica* 38: 625–634.
- RODRIGUEZ-GALIANO, V. F., M. SANCHEZ-CASTILLO, J. DASH, P. M. ATKINSON, AND J. OJEDA-ZUJAR. 2016. Modelling interannual variation in the spring and autumn land surface phenology of the European forest. *Biogeosciences* 13: 3305–3317.
- ROOT, T. L., J. T. PRICE, K. R. HALL, S. H. SCHNEIDER, C. ROSENZWEIG, AND J. A. POUNDS. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421: 57–60.
- ROTHMAN, J. M., C. A. CHAPMAN, AND P. J. van SOEST. 2012. Methods in primate nutritional ecology: A user's guide. *Int. J. Primatol.* 33: 542–566.
- van SCHAIK, C. P., J. W. TERBORGH, AND S. J. WRIGHT. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annu. Rev. Ecol. Syst.* 24: 353–377.
- SCHULZ, J., P. ALBERT, H.-D. BEHR, D. CAPRION, H. DENEKE, S. DEWITTE, B. DÜRR, P. FUCHS, A. GRATZKI, AND P. HECHLER. 2009. Operational climate monitoring from space: the EUMETSAT Satellite Application Facility on Climate Monitoring (CM-SAF). *Atmos. Chem. Phys.* 9: 1687–1709.
- SEIMON, A., AND G. PHILLIPPS. 2011. Regional climatology of the Albertine Rift. *In* A. J. Plumptre (Ed.). *The ecological impact of long-term changes*, pp. 9–31. Nova Science Publishers Inc, New York, NY.
- SHANAHAN, M., S. SO, S. G. COMPTON, AND R. CORLETT. 2001. Fig-eating by vertebrate frugivores: a global review. *Biol. Rev.* 76: 529–572.
- SMART, R. E., S. M. SMITH, AND R. V. WINCHESTER. 1988. Light quality and quantity effects on fruit ripening for Cabernet Sauvignon. *Am. J. Enol. Vitic.* 39: 250–258.
- SMYTHE, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. *Am. Nat.* 104: 25–35.
- SNOW, D. W. 1965. A possible selective factor in the evolution of fruiting seasons in tropical forests. *Oikos* 15: 274–281.
- STAMPONE, M., J. HARTTER, C. A. CHAPMAN, AND S. J. RYAN. 2011. Trends and variability in localized precipitation around Kibale National Park, Western Uganda, Africa. *Res. J. Environ. Earth Sci.* 3: 14–23.
- STENSETH, N. C., AND A. MYSTERUD. 2005. Weather packages: finding the right scale and composition of climate in ecology. *J. Anim. Ecol.* 74: 1195–1198.
- STRUHSAKER, T. T. 1975. The red colobus monkey. University of Chicago Press, Chicago, Illinois.
- STRUHSAKER, T. T. 1997. Ecology of an African rain forest: logging in Kibale and the conflict between conservation and exploitation. University of Florida Press, Gainesville, Florida.
- THOMPSON, M. E., AND R. W. WRANGHAM. 2008. Diet and reproductive function in wild female chimpanzees (*Pan troglodytes schweinfurthii*) at Kibale National Park, Uganda. *Am. J. Phys. Anthropol.* 135: 171–181.
- VISSER, M. D., E. JONGEJANS, N. van BREUGELM, P. A. ZUIDEMA, Y.-Y. CHEN, A. R. KASSIM, AND H. de KROON. 2011. Strict mast fruiting for a

- tropical dipterocarp tree: a demographic cost-benefit analysis of delayed reproduction and seed predation. *J. Ecol.* 99: 1033–1044.
- van VLIET, A., AND M. D. SCHWARTZ. 2002. Phenology and climate: the timing of life cycle events as indicators of climate variability and change. *Int. J. Climatol.* 22: 1713–1714.
- WALTHER, G. R., E. POST, P. CONVEY, A. MENZEL, C. PARMESAN, T. J. C. BEEBEE, J. M. FROMENTIN, O. HOEGH-GULDBERG, AND F. BAIRLEIN. 2002. Ecological responses to recent climate change. *Nature* 416: 389–395.
- WARNER, R. M. 1998. Spectral analysis of time-series data. Guilford Press, New York, New York.
- WHEELWRIGHT, N. T. 1985. Fruit size, gape width, and the diets of fruit-eating birds. *Ecology* 66: 808–818.
- WOLKOVICH, E. M., B. I. COOK, J. M. ALLEN, T. M. CRIMMINS, J. L. BETANCOURT, S. E. TRAVERS, S. PAU, J. REGETZ, T. J. DAVIES, AND N. J. KRAFT. 2012. Warming experiments underpredict plant phenological responses to climate change. *Nature* 485: 494–497.
- WORMAN, C. O., AND C. A. CHAPMAN. 2005. Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. *J. Trop. Ecol.* 21: 689–697.
- WRANGHAM, R. W., C. A. CHAPMAN, A. P. CLARK-ARCADI, AND G. ISABIRYE-BASUTA. 1996. Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In W. C. McGrew, L. F. Marchant, and T. Nishida (Eds.), *Great ape societies*, pp. 45–57. Cambridge University Press, Cambridge, UK.
- WRANGHAM, R. W., N. L. CONKLIN, C. A. CHAPMAN, AND K. HUNT. 1991. The significance of fibrous foods for Kibale Forest chimpanzees. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 334: 171–178.
- WRIGHT, S., AND O. CALDERÓN. 2006. Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. *Ecol. Lett.* 9: 35–44.
- WRIGHT, S. J., AND O. CALDERÓN. 2018. Solar irradiance as the proximate cue for flowering in a tropical moist forest. *Biotropica* 50: 374–383.
- WRIGHT, S. J., AND C. P. VAN SCHAIK. 1994. Light and phenology of tropical trees. *Am. Nat.* 143: 192–199.
- ZHANG, X., S. LIANG, G. ZHOU, H. WU, AND X. ZHAO. 2014. Generating global land surface satellite incident shortwave radiation and photosynthetically active radiation products from multiple satellite data. *Remote Sens. Environ.* 152: 318–332.