BIOTROPICA
THE JOURNAL OF THE ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION

BIOTROPICA 50(3): 431–441 2018 10.1111/btp.12560

Inter-annual variability of fruit timing and quantity at Nouragues (French Guiana): insights from hierarchical Bayesian analyses

Irene Mendoza[1,2,5], **Richard S. Condit**[3], **S. Joseph Wright**[3], **Adeline Caubère**[1], **Patrick Châtelet**[4], **Isabelle Hardy**[1], and **Pierre-Michel Forget**[1]

[1] Muséum National d'Histoire Naturelle, Département Adaptations du Vivant, UMR MECADEV 7179 CNRS-MNHN, 1 Av. du Petit Château, 91800 Brunoy, France

[2] Department of Botany, Institute of Biosciences, São Paulo State University (UNESP), Campus of Rio Claro, Phenology Lab. Avenida 24-A n° 1515, CEP 13506-900 Rio Claro, São Paulo, Brazil

[3] Smithsonian Tropical Research Institute, Apartado, 0843-03092 Balboa, Ancon, Panama

[4] CNRS, USR3456, Laboratoire écologie, évolution, interactions des systèmes amazoniens (LEEISA), 275 Route de Montabo, 97300 Cayenne, France

ABSTRACT

The timing and quantity of fruit production are major determinants of the functioning of a forest community, but simultaneous analyses of both are rare. We analyzed a ten-year dataset (2001–2011) of fruit production for 45 tree and liana species from the Nouragues rain forest, French Guiana. We developed a hierarchical Bayesian approach to determine variation in the timing and quantity of fruit production. Our analysis accommodates missing censuses and quantifies variation at seasonal and inter-annual scales. The fruiting peak of 22 of 45 species occurred during the peak of the rainy season, which is typical for central and eastern Amazon. The timing and quantity of fruit production varied substantially across years in most species, with greater variation in quantity than in timing. The timing of fruit production varied from continuously fruiting species to mast fruiting species that had two or more consecutive years without fruit production. Fully 40% of species were mast fruiting species. The seasonal timing and inter-annual variation in fruiting were unrelated to seed dispersal mode across species. We saw no evidence for directional change in the level of fruit production, the timing of fruit production, or their variances; however, 10 yr is a short record for such analyses.

Abstract in French is available with online material.

Key words: Amazon Basin; dispersal modes; frugivory; long-term monitoring; phenology; rain forest; seed production.

PLANT REPRODUCTION VARIES OVER TIME. Both the timing and the quantity of fruit and flower production vary from year to year, or event to event. Simultaneous analyses of both timing and quantity, however, are rare. In the tropics, most phenology studies have used metrics related to quantity, such as the number of flowering or fruiting species and/or trees (*e.g.*, Chapman *et al.* 2005, Zimmerman *et al.* 2007, Chang-Yang *et al.* 2016) or flower and seed counts (*e.g.*, Wright & Calderón 2006, Norden *et al.* 2007a). Measuring quantity but not timing could lead to erroneous interpretations if counts were done at the same time every year (Pearse *et al.* 2017). In the case of analyses of timing, a different problem arises. Many studies of timing are based on first flowering (or leafing) date, which can be linked to climate change (*e.g.*, Amano *et al.* 2010, Ibáñez *et al.* 2010, Mo *et al.* 2017). Population-level first flowering dates do not tell us whether changes affect a minority of individuals or all individuals in a population (Visser *et al.* 2010). In general, changes in phenology affecting both quantity and timing will have far-reaching consequences for ecosystem functioning, and studying the two in isolation may miss important impacts.

Two factors have hindered phenological studies that cover variation in both quantity and timing, particularly in the tropics. First, statistical tools applied to phenology rarely address both quantity and timing together. Second, long-term phenological monitoring is exceedingly rare in the tropics. To the best of our knowledge, phenology has been monitored for more than 10 yr in only ten, 11, and five sites in the tropical Americas, Africa, and Asia, respectively (Sakai *et al.* 2006, Brearley *et al.* 2007, Cannon *et al.* 2007, Chang-Yang *et al.* 2016, Mendoza *et al.* 2017, Abernethy *et al.* 2018, Adamescu *et al.* 2018, Chapman *et al.* 2018, Chen *et al.* 2018, Kurten *et al.* 2018). In addition, many of tropical phenological studies report qualitative observations of focal trees and lack quantitative monitoring of levels of fruit production. Analytical problems are compounded with monitoring challenges of many tropical studies conducted in remote locations or in countries with chronic political instability (*e.g.,* Adamescu *et al.* 2018, Babweteera *et al.* 2018). In the case of our remote

Received 13 June 2017; revision accepted 21 March 2018.

[5]Corresponding author; e-mail: irene.mendoza.sagrera@gmail.com

study area at Nouragues, French Guiana, 29% of the biweekly censuses were missed due to logistic problems. This imposed the need to develop analyses able to accommodate missing censuses as well as evaluate variation in both quantity and timing.

Phenological time series are non-stationary, non-linear, zero-inflated, and auto-correlated (Keatley & Hudson 2010, Mendoza *et al.* 2017). This limits the use of regression methods. Bayesian modeling is a powerful alternative for overcoming the pitfalls of linear regression models applied to phenology (Dose & Menzel 2004, Keatley & Hudson 2010). Bayesian models allow the flexibility often required in hyperdiverse systems and assess uncertainty beyond frequentist methods (Clark 2005, Condit *et al.* 2013). In addition, hierarchical Bayesian models can incorporate variation at different scales including within and among years (McMahon & Diez 2007, Dietze 2017, Pearse *et al.* 2017). Bayesian analyses also easily accommodate missing data. We developed a hierarchical Bayesian framework to analyze seasonal and inter-annual variation in the timing and quantity of fruit production and applied the framework to 10 yr of fruit production data from Nouragues, French Guiana (see Dose & Menzel 2004, Amano *et al.* 2010, Ibáñez *et al.* 2010, Diez *et al.* 2012, 2014, and Pearse *et al.* 2017 for other Bayesian approaches applied to phenology).

Our primary aim was to quantify the mean date and total fruit production for 45 species over 10 yr. We use inter-annual variation in estimates of fruit production (called hyperparameters in the hierarchical Bayesian framework) and their credible intervals to describe interspecific variation in fruiting synchrony. Inter-annual variation in fruit fall offers a precise measure of masting, while variation in the intra-annual date is a measure of seasonality. We gain insight into when each species produces fruit, and how consistent this is from year to year. The community-wide estimates open the door to a wide variety of hypothesis testing concerning timing, levels of production, and their variation (Janzen 1967, Smythe 1970, Frankie *et al.* 1974, van Schaik *et al.* 1993). As a proof of concept, we evaluate two hypotheses concerning seed dispersal modes and the seasonal and inter-annual variation in levels of fruit production.

METHODS

STUDY SITE.—The phenological monitoring was carried out at the Nouragues Research Station (4°05′ N, 52°40′ W; http://www.nouragues.cnrs.fr), a mature Amazonian forest in the Nouragues National Nature Reserve of French Guiana. Vegetation is dense, lowland, old-growth *terra firme* rain forest. Two physiognomically different forest types can be distinguished: high mature forest (20–35 m height for trees) with an open understory and low forest (<20 m height) with many lianas and a dense understory (Poncy *et al.* 2001). Settlements of native people disappeared from the area in the eighteenth century, and as it is far from navigable watercourses, human impact has been minor during the last two centuries (Charles-Dominique 2001). The research station stands between two geomorphological formations, a tableland of granitic sandy soil on the west and another of clayey soil derived from metavolcanic rock material of the Paramaca formation to the east (Grimaldi & Riéra 2001). A 400 × 300-m plot called *Petit Plateau* (PP) was established on the granitic soil, and a larger plot of 1000 × 1000 m, the *Grand Plateau,* on the clay.

A meteorological station is located in a clearing at the field station at Nouragues. The station was manual from 2003 to 2006 and was then replaced with an automatic station (WS-GP2 Weather Station, DeltaT Devices). Annual rainfall averaged 2727 mm from 2003 to 2011, and there was a 73-day dry season lasting from August to early November during which precipitation averaged between 60 and 100 mm per month (Fig. 1). The

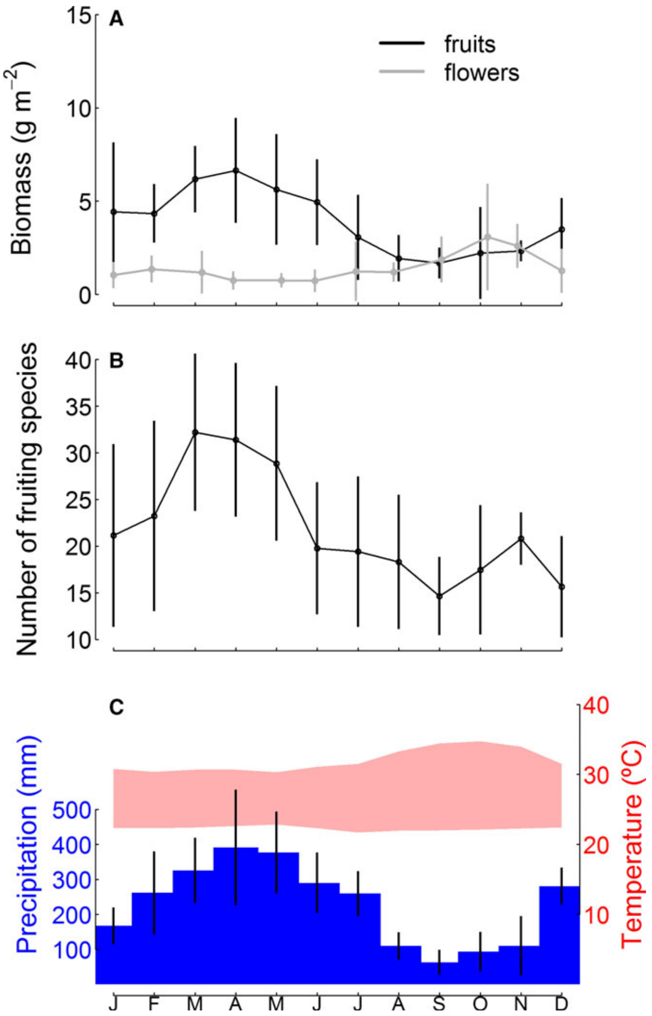

FIGURE 1. Monthly community-level flower and fruit production, temperature, and rainfall at Nouragues, French Guiana. Mean (±1 SD) values of the dry biomass of flowers (gray line) and fruit (black line) across months (panel A). Weights are summed over all species. Mean (±1 SD) values of the number of fruiting species during each month (B). Mean precipitation (blue bars) and mean minimum and maximum temperature (red envelope) (C). Fruit biomass was highly correlated with the number of fruiting species each month (panels A and B) and with rainfall seasonality (panels A and C).

lowest mean monthly rainfall was 63 ± 36 mm (mean ± 1 SD) in September. The mean daily temperature was 27°C (average 2003–2011; Fig. 1).

PHENOLOGICAL DATA.—This study expands a previous five-year analysis of Norden *et al.* (2007a). Our ten-year dataset (from February 2001 until February 2011) includes 22,316 seeds and fruits identified to species. Phenological information was collected using a network of 160 seed traps of 0.5 m^2 (see Wright & Calderón 2006, for the same protocol on Barro Colorado Island, Panama, and Mendoza *et al.* 2015, for a brief description of the methods at Nouragues). Traps were composed of a nylon mesh and suspended 1.5 m aboveground to avoid disturbance by large animals. Twenty traps were set up along five parallel trails on the Grand Plateau (100 traps in total), and fifteen traps were set up along four parallel trails on the Petit Plateau (60 in total). Traps were established randomly along transects, but the minimum distance between neighbors was 15 m. The sampling protocol called for biweekly censuses; however, we missed 75 (29%) of the 260 censuses that should have taken place in 10 yr due to logistical problems. The content of each trap was first separated into flowers and fruits or seeds, then oven-dried at 70°C and weighed using an electronic balance (see Chave *et al.* 2008 for more details). All seeds, fruits, and fragments >5 mm in size collected in traps were determined to species or morphospecies. We excluded species with very tiny seeds that passed through the mesh. Seeds and fruits were characterized as mature (filled endosperm of the seed or entire fruit) versus partly eaten or parasitized by insects. We converted mature fruits into seed counts using the mean number of seeds per fruit calculated using a sample of five fruits from our collection when possible and values from van Roosmalen (1985) for the remaining species. We excluded seeds and fruits that we could not identify to species or morphotype with certainty. We followed the sample size criteria of Wright and Calderón (2006) and restricted our analyses to a subset of 45 species (30 trees and 15 lianas; see Table S1) that had seeds or fruits captured at least in ten different traps in any single year. This criterion ensures that seeds or fruits of each species come from multiple seed-bearing plants. We measured the length and width of five seeds of each species using digital calipers.

SPECIES-SPECIFIC MODELS OF SEED PRODUCTION.—The underlying model describes the number of seeds counted as a function of the day, for a single species in a single year. We assume a Gaussian function describes this,

$$S_d = P\ \mathrm{Norm}\ (d,\ \mathrm{mean} = \mathrm{peakday}, \mathrm{SD} = \varepsilon), \tag{1}$$

where S_d is the number of seeds falling on day *d*. The parameter *peakday* is the day of peak seedfall, which is the mean of the Gaussian function; ε is the standard deviation, which quantifies the inverse of fruiting synchrony; and *P* is total annual seedfall. Norm indicates a Gaussian probability density, which integrates to one, so that *P* is the integral of the seed production curve or the estimated number of seeds falling into an area equal to all the traps. We then scaled up to total trap area (80 m^2) for graphical presentation only, as this is identical for every species. This model therefore overcomes the problem of missing censuses, as the accumulated amount of seeds is distributed all over the year according to a Gaussian function.

Estimating the three parameters of equation (1) required a likelihood function describing the probability of observed daily seed counts, C_d, given the daily prediction S_d. We used a negative binomial link function,

$$C_d = \mathrm{NegBinom}\ (\mathrm{mean} = S_d,\ \mathrm{clump} = k)), \tag{2}$$

a standard tool for handling aggregate (*i.e.,* zero-inflated) abundance data. The parameter *k* is the clumping parameter and must be fitted as well. The calculation of the likelihood of parameters *P* and *peakday* included both the negative binomial of observed seed counts (equation 2), and probabilities from their respective hyperdistributions (equations 3–4). We assumed the parameters ε and *k* were constant across all years for each species.

The hierarchical component was defined across years within a species. The parameter *peakday* has a different estimate each year, and $peakday_t$ means the mean date of seedfall in year *t*. Likewise, the parameter P_t has an estimate in each year. We assumed both parameters were drawn from their own hyperdistribution,

$$\mathrm{peakday}_t \sim \mathrm{Norm}\ (\mathrm{mean} = \mu, \mathrm{SD} = \sigma), \tag{3}$$

$$\log(P_t) \sim \mathrm{Norm}\ (\mathrm{mean} = \log(\mu), \mathrm{SD} = \log(\sigma)). \tag{4}$$

The four hyperparameters—μ, σ, $\log(\mu)$, $\log(\sigma)$—were fitted using the ten yearly estimates of $peakday_t$ and P_t.

To fit reproductive curves across years, it was necessary to use the same annual daily numbering each year (*i.e.,* 1 . . . 365 or 366). As long as reproduction happened in only part of the year and not near day 1 January, it was straightforward to fit the annual curves and their multi-year hyperdistribution with day 1 on 1 January. But for a species reproducing around 1 January, daily numbering must be redefined. We defined the calendar year for each species so that day 182 corresponded with the time of peak fruit production. For example, if a species fruits around 1 February, its year began with day 1 on 1 August and ended with day 365 on 31 July. This required an initial estimate of the peak fruiting date based on the sum of seed fall for each day of the year overall 10 yr. Once all analyses were finished, we back translated dates so that years began on 1 January for display purposes. We discarded data from 2001 to 2011 for species that produced fruit near when the censuses started and ended (February 2001 and 2011, respectively).

Posterior distributions of the species-specific parameters of the seed production model as well as the hyperparameters were obtained with Metropolis–Hasting algorithms, using 10,000 iterations and a 1000-iteration burn-in period (see Condit *et al.* 2013 for more details). Priors were assumed to be non-informative, that is every valid parameter was equally likely. Chains were inspected visually for mixing. The mean and the 2.5th and 97.5th percentiles were taken as the best estimate for a parameter and credible intervals, respectively.

We used chi-squared analyses to compare the number of species that fruited during dry versus wet season, according to dispersal modes. The fruiting season of each species was determined using the hypermean μ of seed production (fruiting during August to November belonged to the dry season and the rest of months to the wet season). We classified inter-annual variation in the seasonal timing of fruit production according to values of the hyper-standard-deviation σ of *peakday*: *low* means species with values in the first quartile, *medium* for values among the second and third quartiles, and *high* refers to values in the fourth quartile. We performed a non-parametric Spearman rank test to understand whether there is an association between variability in timing, quantified by σ, or seed production, expressed by $\log(\sigma)$, and the dispersal mode of species. Species were classified as *masting* if there were at least two consecutive years with annual values of P and their credible intervals close to zero (see Norden *et al.* 2007a for the same criterion). All analyses were performed with the statistical language R, v. 3.3.2 (R Development Core Team 2016), and all our code is available at a Git repository (https://doi.org/10.5281/zenodo.1235013).

RESULTS

ANNUAL SEASONALITY OF SEED PRODUCTION.—Fruit production at Nouragues was seasonal, with a peak in both total fruit dry biomass and number of fruiting species during March–May (Fig. 1A and B). Mean monthly rainfall was positively correlated with mean fruit biomass (Pearson's correlation test: $r = 0.89$ and $P < 0.0001$) and mean number of fruiting species ($r = 0.74$ and $P = 0.006$). The peak of fruit production coincides with the peak of the rainy season. In contrast, flower dry biomass peaks in the late dry season from September to November ($r = -0.72$ and $P = 0.007$).

Our hierarchical models of seed production corroborated this seasonal pattern. Twenty-two of 45 species had their hypermean for *peakday* (μ) during the peak of the rainy season from March to May (Fig. 2; Table S2). The seasonal pattern of seed production did not differ among dispersal modes, with virtually the same proportion of species with abiotic and biotic dispersal modes having their fruiting peaks during the rainy versus the dry season (Figs. 2 and 3; $\chi^2 = 0.01$; $P < 0.9$; df = 1).

WITHIN-YEAR SYNCHRONY OF SEED PRODUCTION.—The standard deviation of the date of seed fall within a year, ε, had a median value of 37.8 days across the 45 species. Five species had $\varepsilon > 80$ days, a value large enough to suggest fruit fell for much of the year, and indeed, four of those five species fruited over much of the year. In the most extreme case, *Mimosa guilandinae* produced fruit nearly continuously from June 2001 to November 2010. *Mimosa, Coccoloba excelsa,* and *Terminalia guyanensis* had seeds in traps in every calendar month.

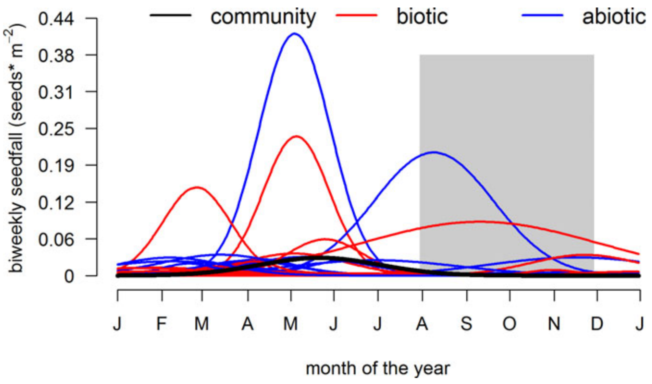

FIGURE 2. Species-level seed production in Nouragues across the year. The horizontal axis indicates the months of the year and the vertical axis represents daily seed count for each species estimated using fitted values of the hyperparameters for productivity, *P*, and timing, *peakday*. Blue curves represent abiotically dispersed species, red curves biotic. The thick black line represents mean productivity and timing values across species (labeled 'community'). The gray rectangle represents the dry season.

INTER-ANNUAL VARIATION IN THE TIMING OF SEED PRODUCTION.—We classified species as having *low* variation in fruit production among years if σ, the fitted value of the hyperparameter for the standard deviation of *peakday,* was less than 25 days, *medium* for values between 25 and 65 days and *high* for species with values larger than 65 days (Table 1 and Fig. 3). Variability in timing did not differ significantly between dispersal modes ($r_S = 0$; $F = 0.14$; $P > 0.7$). The most constant species with respect to timing was *Virola michelii* (Fig. 4), which fruited in late January and early February each year and had a fitted σ value of just 8.8 days (Table S2). At the other extreme, five species had fitted σ values larger than 90 days (*e.g., Vochysia guianensis* and *Manilkara huberi*; Table S2). For $\sigma = 90$, the fitted Gaussian hyperdistribution of *peakday* indicates 65% of mean annual dates of fruit fall can be expected to fall in a six-month window (Fig. 3).

INTER-ANNUAL VARIATION IN THE QUANTITY OF SEED PRODUCTION.—Fitted values of the standard deviation of the hyperdistribution for annual seed fall, $\log(\sigma)$, showed large values for most species (median = 2.82, min = 0.6; max = 7.4; Table S2), indicating high inter-annual variation of seed production. Species showing values of $\log(\sigma)$ smaller than 1 on a logarithmic scale (namely *M. hoffmannseggiana*, *M. guilandinae*, *Q. duckei*, *R. frutescens, S. acreanum*, and *V. micheli*) also presented relatively small credible intervals for variation in annual values of seed fall (P) across years (Table S3). *Manilkara bidentata* and *Licania membranacea* are conspicuous examples of large variability in seed production (Fig. 4 and Table S3). *Manilkara bidentata* had one big fruiting year in 2010, but produced only trivial quantities of fruit in the remaining 9 yr. Similarly, *L. membranacea* produced large amounts of seeds in 2002, had other two secondary seed pulses in 2008 and 2009, and seed production was almost negligible for the rest of the time series (Fig. 4 and Table S3). These are masting species with

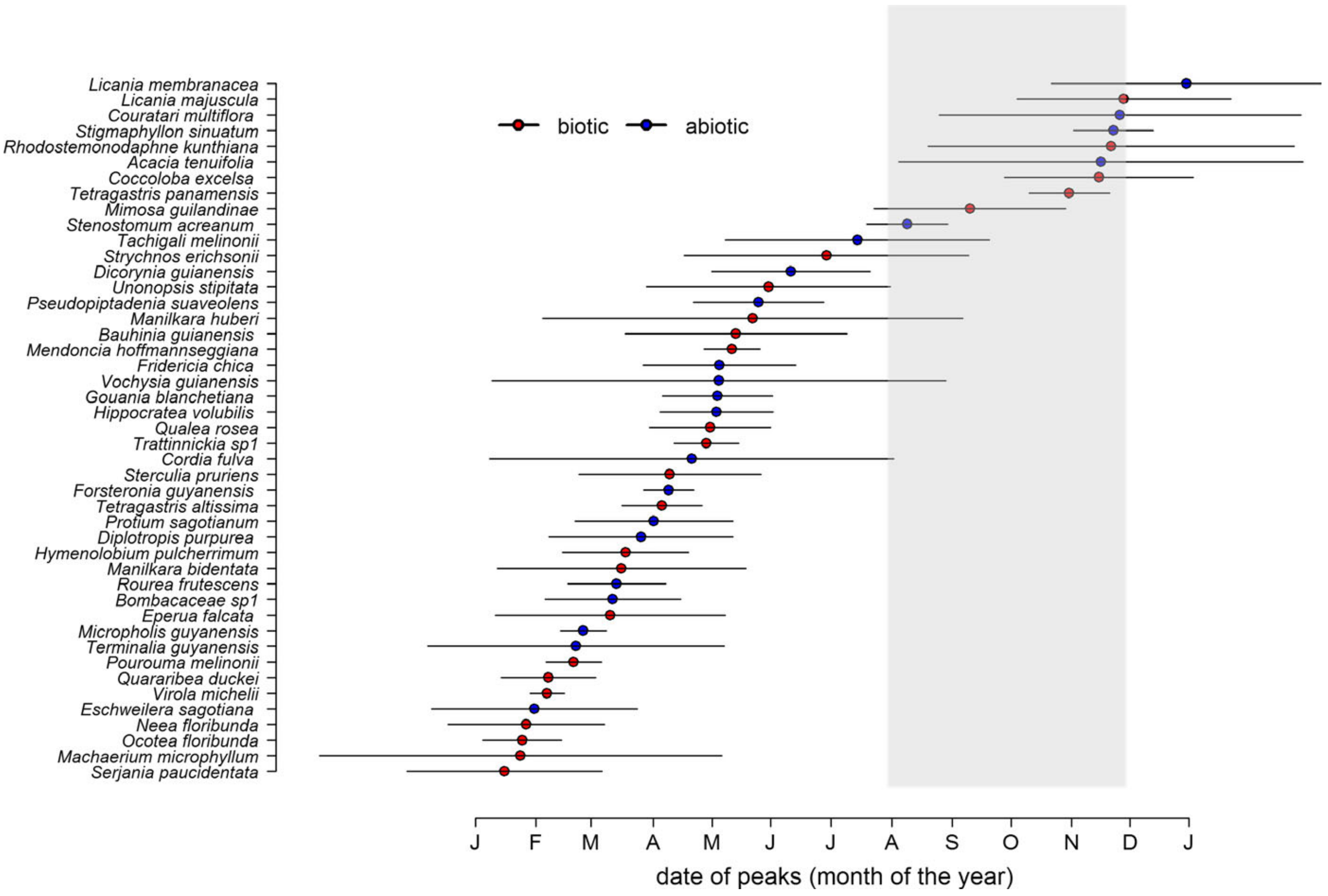

FIGURE 3. Species ranked according to their mean dates of seed fall across years (*i.e.*, the hypermean of *peakday* or μ). Most species had their peak of seed production during the early rainy season (March–May). Few species fruited through most of the dry season (gray panel). Error bars show the hyper–standard-deviation, σ, of *peakday*. Red and blue dots represent biotic and abiotic seed dispersal modes, respectively.

synchronized, supra-annual production of large seed crops, and scattered seed production in other years. According to our definition (at least two consecutive years without seed production), 40% or 18 species were classified as masting, including *Sterculia pruriens*, both *Manilkara* spp., both *Licania* spp., *Tachigali melionii*, *Qualea rosea*, and *Vochysia guianensis* (Table 1). Variability in seed production, $log(\sigma)$, did not differ significantly between dispersal modes ($r_S = 0$; $F = 0.24$; $P > 0.62$).

We found a positive relationship between annual variation in fruit production and annual variation in fruiting date. The hyper-standard-deviation $\log(\sigma)$ of P and σ of *peakday* was positively correlated (Fig. 5; Pearson's correlation test: $r = 0.64$ and $P < 0.001$). This means that those species with more irregular patterns in the quantity of seed production (*e.g.*, *M. huberi, V. guianensis,* or *R. kuntiana*) also showed more intra-annual (*i.e.*, seasonal) variation in the timing of those peaks (Table S2).

DISCUSSION

There have been few long-term studies reporting quantitative values of fruit phenology in the tropics, even though fruit production is essential for frugivores, granivores and plant regeneration, and shifts in fruit crops are anticipated under a changing atmosphere and climate. We used a hierarchical Bayesian model to analyze seasonal and inter-annual variation in the timing and levels of fruit production for 10 yr for 45 tree and liana species from Nouragues, French Guiana. Previous phenological studies in Guianan forests have been for five or fewer years (Zhang & Wang 1995, Norden *et al.* 2007a) or focused on a single species (Jesel 2005). Diaz-Martin *et al.* (2014) reported 8 yr of seed production for a site in the Peruvian Amazon. To the best of our knowledge, ours is the longest study with quantitative estimates of seed production in the Amazon Basin.

ANNUAL SEASONALITY.—The annual peak of fruit production at the community level was associated with the peak of the annual wet season from March to May. In contrast, the annual peak of flower biomass appeared during the driest months in September and October. The community-level seasonality of fruit production was corroborated by our analysis of species-level fruit production, with the estimated mean date of annual seed fall (*peakday* in

TABLE 1. *Fruiting patterns of the 45 study species. We classified species according to variation in the timing of seed production, using quartiles of the distribution of the hyper-standard-deviation* σ *of the mean date of seedfall,* peakday*:* low *means species with values in the first quartile,* medium *for values among the second and third quartiles, and* high *refers to values in the fourth quartile. We classified species as masting if there were at least two continuous years without seed production, according to annual values of* P *and their credible intervals (see Norden* et al. *2007a for the same criterion).*

Species	Dispersal syndrome*	Inter-annual variability on timing of seed production	Masting behavior	Season when fruiting
Acacia tenuifolia	ane	High	No	Wet
Bauhinia guianensis	bal	Medium	No	Wet
Bombacaceae sp1	ane	Medium	No	Wet
Coccoloba excelsa	zoo	Medium	No	Dry
Cordia fulva	zoo	High	Yes	Wet
Couratari multiflora	ane	High	Yes	Dry
Dicorynia guianensis	ane	Medium	No	Wet
Diplotropis purpurea	ane	Medium	Yes	Wet
Eperua falcata	bal	Medium	Yes	Wet
Eschweilera sagotiana	zoo	Medium	Yes	Wet
Forsteronia guyanensis	ane	Low	No	Wet
Fridericia chica	bal	Medium	No	Wet
Gouania blanchetiana	ane	Medium	No	Wet
Hippocratea volubilis	ane	Medium	No	Wet
Hymenolobium pulcherrimum	ane	Medium	No	Wet
Licania majuscula	zoo	Medium	Yes	Dry
Licania membranacea	zoo	High	Yes	Wet
Machaerium microphyllum	ane	High	Yes	Wet
Manilkara bidentata	zoo	High	Yes	Wet
Manilkara huberi	zoo	High	Yes	Wet
Mendoncia hoffmannseggiana	zoo	Low	No	Wet
Micropholis guyanensis	zoo	Low	No	Wet
Mimosa guilandinae	ane	Medium	No	Dry
Neea floribunda	zoo	Medium	Yes	Wet
Ocotea floribunda	zoo	Low	No	Wet
Pourouma melinonii	zoo	Low	No	Wet
Protium sagotianum	zoo	Medium	No	Wet
Pseudopiptadenia suaveolens	ane	Medium	No	Wet
Qualea rosea	ane	Medium	Yes	Wet
Quararibea duckei	zoo	Medium	No	Wet
Rhodostemonodaphne kunthiana	zoo	High	Yes	Dry
Rourea frutescens	zoo	Medium	No	Wet
Serjania paucidentata	ane	Medium	No	Wet
Stenostomum acreanum	zoo	Low	No	Wet
Sterculia pruriens	zoo	Medium	Yes	Wet
Stigmaphyllon sinuatum	ane	Low	No	Dry
Strychnos erichsonii	zoo	High	No	Wet
Tachigali melinonii	ane	High	Yes	Wet
Terminalia guyanensis	ane	High	No	Wet
Tetragastris altissima	zoo	Low	Yes	Wet
Tetragastris panamensis	zoo	Low	No	Dry
Trattinnickia sp1	zoo	Low	No	Wet
Unonopsis stipitata	zoo	Medium	Yes	Wet
Virola michelii	zoo	Low	No	Wet
Vochysia guianensis	ane	High	Yes	Wet

*Dispersal modes: *ane* = anemochorous, *bal* = ballistic, and *zoo* = zoocho.

equation 1) falling between March and May for 22 of 45 abundant species.

The pattern of fruiting seasonality at Nouragues with a peak during the rainy season has been described for other lowland forests in French Guiana (Sabatier 1985, Sabatier & Puig 1986) and for seasonally dry forests in the central and eastern Amazonia (Alencar *et al.* 1979, Peres 1994, Barlow *et al.* 2007, Bentos *et al.* 2008). In contrast, in the forests of southern Mesoamerica, fruit production peaks in the driest months (Frankie *et al.* 1974, Wright & Calderón 2006), with a secondary fruiting peak during the rainy season (see Morellato *et al.* 2013 for a complete description). Community-level fruit production is bimodal, with one peak during the early rainy season and another near the end of the rainy season at Cocha Cashu, Peru (Terborgh 1983, Diaz-Martin *et al.* 2014). This bimodal pattern also appears in Guyana, with greater fruit production during the wettest month in February–May (Ter Steege & Persaud 1991, Thomas 1999). The monthly mean number of fruiting species peaked in January in Paracou, French Guiana; 1 mo later in Guyana; and 2 mo later in Panama (Forget *et al.* 2002). These differences might be related to the movements of the Inter-tropical Convergence Zone (ITCZ), with peak fruit production occurring shortly before the ITCZ brings rains that favor seedling establishment and clouds that reduce light availability (van Schaik *et al.* 1993, Wright & van Schaik 1994).

An increase in solar radiation reaching the forest during the dry season might trigger flowering of some species at Nouragues (see Wright & Calderòn 2018) and contribute to peak community-level flowering observed in the dry season. Flowering during the dry season might also improve pollination given that other resources (*i.e.*, young leaves and fruit) are scarce and the warm dry season temperatures are likely to encourage insect activity (Janzen 1967). In addition, seed dispersal during the rainy season enables germination and initial root growth at the wettest time of

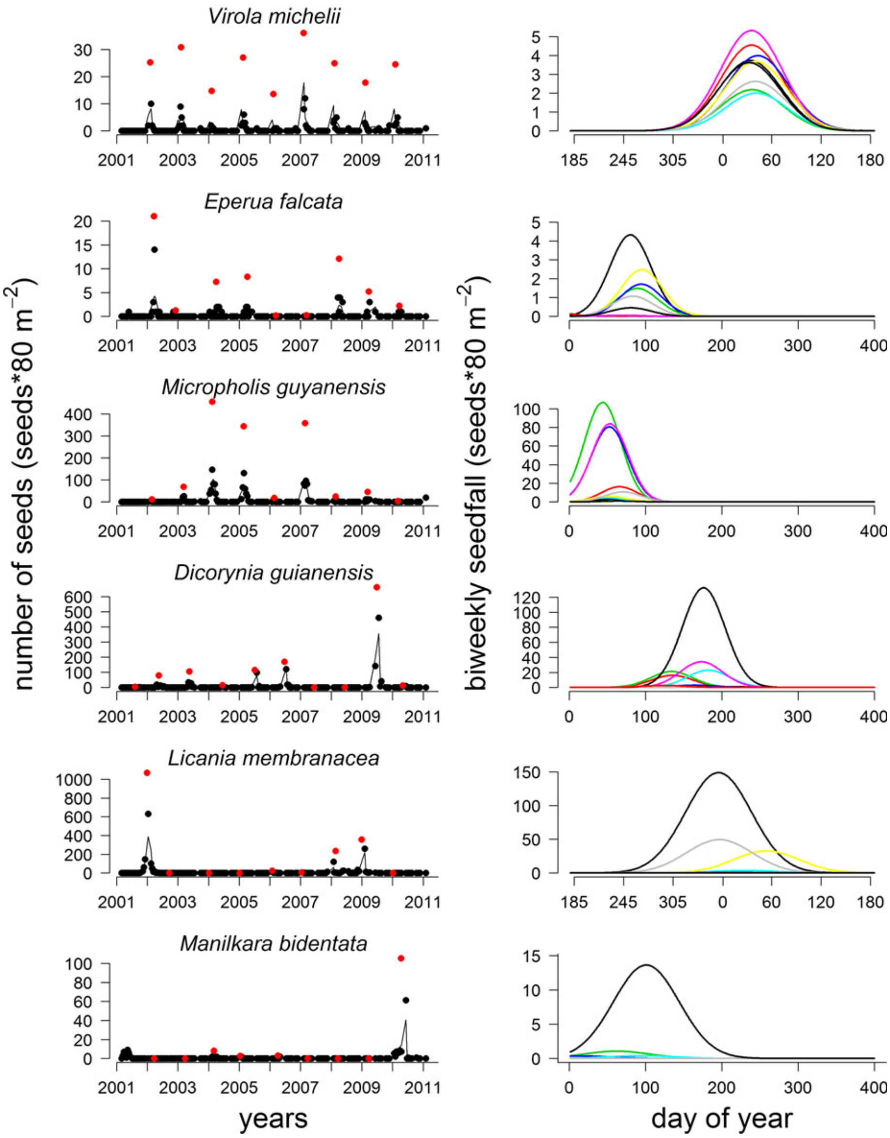

FIGURE 4. Seed production for six of the 45 species studied in Nouragues for the 2001–2011 period. Panels on the left show the linear time series across the 10 yr; black points represent raw data, red dots the estimated sum of seed production per year (the parameter P_i). The right panel shows the fitted production curve (biweekly seed count) for all 10 yr, based on the estimated annual seed curves. Colors indicate different years. The species are ordered from the most consistently fruiting species at the top (*Virola michelii*) to the most irregularly fruiting species at the bottom (*Manilkara bidentata*).

year, with germination peaking in June and July at Nouragues (Norden *et al.* 2007b). The time required for fruit development after flowering might also push the fruiting peak into the rainy season. Unfortunately, we did not identify flowers to species so we were unable to evaluate the transition time from flowers to fruits at the species level.

INTER-ANNUAL VARIATION IN SEED PRODUCTION.—Inter-annual variation in the quantity of fruit produced increased with intra-annual variation in the seasonal timing of fruit production. This is a previously unknown result made possible by simultaneous quantification of the timing and level of production in a hierarchical, Bayesian model. Inter-annual variation in community-level seed production is extreme in the Dipterocarp forests of Southeast Asia where hundreds of species from dozens of families reproduce at irregular, multi-year intervals in general flowering events. At many sites, general flowering events can occur at two times during the year separated by approximately 6 mo (Sakai *et al.* 2006, Numata *et al.* 2013). It is possible that inter-annual variation in the level of fruit production and intra-annual variation in the seasonal timing of fruit production increase together elsewhere. More studies that evaluate seasonal timing and levels of production will be needed to evaluate this possibility.

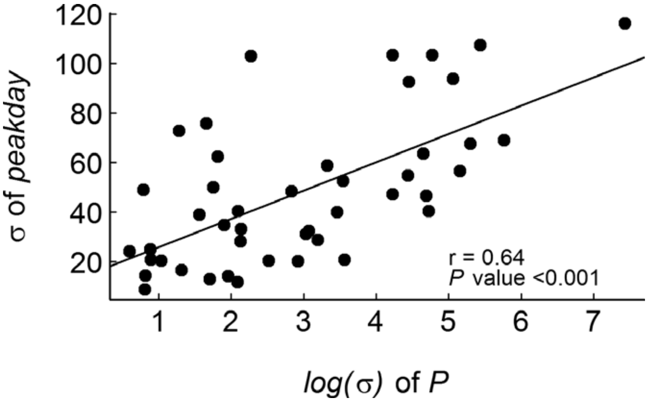

FIGURE 5. Scatterplot showing the correlation between hyperparameters log (σ) of P and σ of *peakday*. The significant, positive relationship indicates that species with more variable quantities of inter-annual seed production also tend to have more variable seasonal timing of seed production.

Virola michelii was the least variable species in our dataset for timing and quantity (Fig. 4, Fig. S1). *Virola michelii* fruited in late January and early February, which is earlier than the community-level fruiting peak. A possible explanation of this markedly constant pattern of *V. michelii* is that the species has been selected to fruit when there is low fruit diversity and productivity, thus increasing dispersal chances (Snow 1965). The aril is rich in lipids and is a valuable resource for a variety of large, competitively dominant frugivores, including spider monkeys, toucans and other large birds (Ratiarison & Forget 2013). Few seeds are wasted, with the majority of seed being dispersed away from the mother tree (Ratiarison & Forget 2013, Boissier *et al.* 2014). Congeners have similar fruiting seasonality, fruit traits and seed dispersal agents on Barro Colorado Island, Panama (Howe 1981, Howe & Vande Kerckhove 1981).

Mast fruiting has been considered a rare strategy in the tropics (Kelly & Sork 2002). With mast fruiting defined as failure to fruit in two or more consecutive years, we found that 40% of species were mast fruiters at Nouragues. Our study confirms and extends the conclusion that mast fruiting is commonplace at Nouragues (Norden *et al.* 2007a), with five additional years of data. Inter-annual variation in seed production is also substantial on Barro Colorado Island, Panama, although still lower than at higher latitudes (Wright *et al.* 2005). Mast fruiting might increase seed survival, with large, synchronous seed crops satiating seed predators (Kelly & Sork 2002), although satiation of dispersers is also possible (Mendoza *et al.* 2015).

Dispersal mode (biotic vs. abiotic) was unrelated to the seasonal timing of fruiting and to inter-annual variation in levels of fruit production at Nouragues. Elsewhere wind-dispersed species tend to disperse their seeds during the dry season when wind speeds are greatest and reduced canopy leaf area lowers impediments to dispersal by wind (Janzen 1967, van Schaik *et al.* 1993, Griz & Machado 2001). Unfortunately, we lack wind data from Nouragues and cannot assess the association between dispersal mode and seasonal winds. It has also been hypothesized that inter-annual variation in levels of seed production is greater for wind-dispersed than for animal dispersed species because seeds cannot saturate the wind (Janzen 1974).

CAVEATS.—As a highlight of our study, the hierarchical Bayesian approach that we developed proved to be a useful tool for quantifying intra- and inter-annual variability in the timing and levels of seed production at the specific level. Models accommodated missing censuses and were flexible enough to describe the fruiting phenology of most species; however, there were problems with continuously fruiting species. The model correctly captured aseasonality as a large within-year variance, but the estimated mean date of fruiting becomes meaningless (see *Mimosa guilandinae* in Fig. S1). There is an additional problem for species that fruit more than once each year. Continuous and multimodal fruit production was rare at Nouragues, but can be more common in aseasonal forests (Newstrom *et al.* 1994). Our model cannot accommodate multimodal phenologies; however, an appropriate Bayesian model is possible. We did not consider phylogenetic dependence, which can be an important factor determining phenological patterns and fruit characteristics (Herrera 1992, Staggemeier *et al.* 2017) because 45 species is a small sample size for phylogenetic analyses.

Ten years represents a significant improvement in the duration of monitoring of seed production in Amazonian forests, but we clearly need longer periods. Several masting species only produced ample fruit in one of 10 yr, meaning we have only a poor understanding of their productivity. To understand the influence of large inter-annual climatic events such ENSO or directional trends through time, we will need many more years of data, because ENSO has a typical frequency of 2–5 yr (Hu *et al.* 2017). We can see no evidence for directional change in the level of fruit production, the timing of fruit production or their variances in our data (Fig. 4, Fig. S1); however, 10 yr is a short record for such analyses. Future climatic models predict more frequent extreme climatic conditions (IPCC 2013), and we still do not know how this will affect tropical forest plants. Shifts in both fruiting quantity and timing might have dramatic consequences for frugivores, granivores, and seed fate (Mendoza *et al.* 2015, Morellato *et al.* 2016). We need longer phenological records from Amazonia as well as other tropical areas (Abernethy *et al.* 2018). The combination of long-term monitoring of plant phenology and local climate, detailed studies of the physiological mechanisms behind reproduction and seedling emergence, compelling statistical tools, and multidisciplinary research including climatologists, physiologists, and ecologists will be required to understand the implications of a changing atmosphere and climate for tropical forest plants.

ACKNOWLEDGMENTS

We thank Stephen Brewer (Chateaubriand Post-doctoral fellowship) for his help installing the 160 seed traps in 2001. I.M. was funded by a postdoctoral fellowship at the MNHN in France by

Fundación Caja Madrid and the Spanish Ministry of Education (reference EX2009-0711), and by a Brazilian FAPESP fellowship (#2012/21601-0) during final writing of this paper. The long-term monitoring at Nouragues received financial and logistic support from the Centre National de Recherche Scientifique (CNRS Nouragues and INEE) and the UMR MECADEV 7179 in France. P. Jordano hosted I.M. at Doñana Biological Station (CSIC) at several phases of the writing of this manuscript.

DATA AVAILABILITY

The data used in this study are archived at a Smithsonian Repository (https://doi.org/10.25570/stri/10088/35071) and the R scripts used for analyses are available at a Git repository (https://doi.org/10.5281/zenodo.1235013; Mendoza *et al.* 2018).

SUPPORTING INFORMATION

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

FIGURE S1. Seed production for the 45 species analyzed in Nouragues during the 2001–2011 period.

TABLE S1. *List of the 45 taxa included in this study.*

TABLE S2. *Hyperparameters of the model for the 45 species included in this study.*

TABLE S3. *Best estimates and credible intervals for peakday and production parameters for the 45 species included in this study.*

LITERATURE CITED

Abernethy, K. A., E. R. Bush, P.-M. Forget, I. Mendoza, and L. P. C. Morellato. 2018. Current issues in tropical phenology: A synthesis. Biotropica 50: 477–482.

Adamescu, G. S., A. J. Plumptre, K. A. Abernethy, L. Polansky, E. R. Bush, C. A. Chapman, L. P. Shoo, A. Fayolle, K. R. L. Janmaat, M. M. Robbins, H. J. Ndangalasi, N. J. Cordeiro, I. C. Gilby, R. M. Wittig, T. Breuer, M. B.-N. Hockemba, C. M. Sanz, D. B. Morgan, A. E. Pusey, B. Mugerwa, B. Gilagiza, C. Tutin, C. E. N. Ewango, D. Scheil, E. Dimoto, F. Baya, F. Bujo, F. Ssali, J.-T. Dikangadissi, K. Jeffery, K. Valenta, L. E. White, M. Masozera, M. L. Wilson, R. Bitariho, S. T. N. Ebika, S. Gourlet-Fleury, and C. M. Beale. 2018. Annual cycles are the most common reproductive strategy in African tropical tree communities. Biotropica 50: 418–430.

Alencar, J. C., R. A. Almeida, and N. P. Fernandes. 1979. Fenologia de espécies florestais em floresta tropical úmida de terra firme na Amazônia Central. Acta Amazon 1: 63–97.

Amano, T., R. J. Smithers, T. H. Sparks, and W. J. Sutherland. 2010. A 250-year index of first flowering dates and its response to temperature changes. Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci. 277: 2451–2457.

Babweteera, F., A. Plumptre, G. S. Adamescu, L. P. Shoo, C. M. Beale, P. Nyeko, and G. Muhangusi. 2018. The ecology of tree reproduction in an African medium altitude rain forest. Biotropica 50: 405–417.

Barlow, J., T. A. Gardner, I. S. Araujo, T. C. Avila-Pires, A. B. Bonaldo, J. E. Costa, M. C. Esposito, L. V. Ferreira, J. Hawes, M. M. Hernandez, M. S. Hoogmoed, R. N. Leite, N. F. Lo-Man-Hung, J. R. Malcolm, M. B. Martins, L. A. M. Mestre, R. Miranda-Santos, A. L. Nunes-Gutjahr, W. L. Overal, L. Parry, S. L. Peters, M. A. Ribeiro-Junior, M. N. F. da Silva, C. D. S. Motta, and C. A. Peres. 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proc. Natl Acad. Sci. USA 104: 18555–18560.

Bentos, T. V., R. C. G. Mesquita, and G. B. Williamson. 2008. Reproductive phenology of Central Amazon pioneer trees. Trop. Conserv. Sci. 1: 186–203.

Boissier, O., A. Bouiges, I. Mendoza, F. Feer, and P.-M. Forget. 2014. Rapid assessment of seed removal and frugivore activity as a tool for monitoring the health status of tropical forests. Biotropica 46: 633–641.

Brearley, F. Q., J. Proctor, L. Surianta, G. Dalrymple Nagy, and B. C. Voysey. 2007. Reproductive phenology over a 10-year period in a lowland evergreen rain forest of central Borneo. J. Ecol. 95: 828–839.

Cannon, C. H., L. M. Curran, A. J. Marshall, and M. Leighton. 2007. Long-term reproductive behaviour of woody plants across seven Bornean forest types in the Gunung Palung National Park (Indonesia): Suprannual synchrony, temporal productivity and fruiting diversity. Ecol. Lett. 10: 956–969.

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., L. J. Chapman, T. T. Struhsaker, 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., K. Valenta, T. Bonnell, K. Brown, and L. Chapman. 2018. Solar radiation and ENSO predict fruiting phenology patterns in a 15-year record from Kibale National Park, Uganda. Biotropica 50: 384–395.

Charles-Dominique, P. 2001. The field station. In F. Bongers, P. Charles-Dominique, P.-M. Forget, and M. Théry (Eds.). Nouragues: Dynamics and plant-animal interactions in a neotropical rainforest, pp. 1–8. Kluwer, Boston, Massachusetts.

Chave, J., J. Olivier, F. Bongers, P. Chatelet, P.-M. Forget, P. van der Meer, N. Norden, B. Riera, and P. Charles-Dominique. 2008. Above-ground biomass and productivity in a rain forest of eastern South America. J. Trop. Ecol. 24: 355–366.

Chen, Y.-Y., A. Satake, I. F. Sun, Y. Kosugi, M. Tani, S. Numata, S. P. Hubell, C. Fletcher, M. N. Nur Supardi, and S. J. Wright. 2018. Species-specific flowering cues among general flowering *Shorea* species at the Pasoh Research Forest. Malaysia. J. Ecol. 106: 586–598.

Clark, J. S. 2005. Why environmental scientists are becoming Bayesians. Ecol. Lett. 8: 2–14.

Condit, R., B. M. J. Engelbrecht, D. Pino, R. Pérez, and B. L. Turner. 2013. Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. Proc. Natl Acad. Sci. USA 110: 5064–5068.

Diaz-Martin, Z., V. Swamy, J. Terborgh, P. Alvarez-Loayza, and F. Cornejo. 2014. Identifying keystone plant resources in an Amazonian forest using a long-term fruit-fall record. J. Trop. Ecol. 30: 291–301.

Dietze, M. C. 2017. Ecological forecasting. Princeton University Press, Princeton, New Jersey.

Diez, J. M., I. Ibáñez, A. J. Miller-Rushing, S. J. Mazer, T. M. Crimmins, M. A. Crimmins, C. D. Bertelsen, and D. W. Inouye. 2012. Forecasting phenology: From species variability to community patterns. Ecol. Lett. 15: 545–553.

Diez, J. M., I. Ibáñez, J. A. Silander, R. Primack, H. Higuchi, H. Kobori, A. Sen, and T. Y. James. 2014. Beyond seasonal climate: Statistical estimation of phenological responses to weather. Ecol. Appl. 24: 1793–1802.

Dose, V., and A. Menzel. 2004. Bayesian analysis of climate change impacts in phenology. Global Change Biol. 10: 259–272.

Forget, P. M., D. S. Hammond, T. Milleron, and R. Thomas. 2002. Seasonality of fruiting and food hoarding by rodents in Neotropical forests: Consequences for seed dispersal and seedling recruitment. In

D. J. Levey, and W. R. Silva and M. Galetti (Eds.). Seed dispersal and frugivory: Ecology, evolution and conservation, pp. 241–256. CABI Publishing, Wallingford, UK.

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.

Grimaldi, M., and B. Riéra. 2001. Geography and climate. In F. Bongers, P. Charles-Dominique, P.-M. Forget, and M. Théry (Eds.). Nouragues: Dynamics and plant animal interactions in a neotropical rainforest, pp. 9–18. Kluwer, Boston, Massachusetts.

Griz, L. M. S., and I. C. S. Machado. 2001. Fruiting phenology and seed dispersal syndromes in Caatinga, a tropical dry forest in the northeast of Brazil. J. Trop. Ecol. 17: 303–321.

Herrera, C. M. 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns – Character syndromes in Mediterranean woody-plants. Am. Nat. 140: 421–446.

Howe, H. F. 1981. Dispersal of a Neotropical nutmeg (*Virola sebifera*) by birds. Auk 98: 88–98.

Howe, H. F., and G. A. Vande Kerckhove. 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. Ecology 62: 1093–1106.

Hu, Z.-Z., A. Kumar, B. Huang, J. Zhu, and H.-L. Ren. 2017. Interdecadal variations of ENSO around 1999/2000. J. Meteorol. Res. 31: 73–81.

Ibáñez, I., R. B. Primack, A. J. Miller-Rushing, E. Ellwood, H. Higuchi, S. D. Lee, H. Kobori, and J. A. Silander. 2010. Forecasting phenology under global warming. Philos. Trans. R. Soc. Lond. Ser. B: Biol. Sci. 365: 3247–3260.

IPCC. 2013. Climate change, 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the IPCC. Cambridge University Press, Cambridge, UK.

Janzen, D. H. 1967. Synchronization of sexual reproduction of trees within dry season in Central America. Evolution 21: 620–637.

Janzen, D. H. 1974. Tropical Blackwater Rivers, animals, and mast fruiting by the Dipterocarpaceae. Biotropica 6: 69–103.

Jesel, S. 2005. Écologie et dynamique de la régéneration de *Dicorynia guianensis* (Cesalpiniaceae) dans une fôret guyanaise. PhD dissertation. Institut National Agronomique Paris-Grignon.

Keatley, M. R., and I. L. Hudson. 2010. Introduction and overview. In I. L. Hudson, and M. R. Keatley (Eds.). Phenological research: Methods for environmental and climate change analysis, pp. 1–22. Springer, Dordrecht, The Netherlands.

Kelly, D., and V. L. Sork. 2002. Mast seeding in perennial plants: Why, how, where? Annu. Rev. Ecol. Syst. 33: 427–447.

Kurten, E. L., S. Bunyavejchewin, and S. J. Davies. 2018. Phenology of a dipterocarp forest with seasonal drought: Insights into the origin of general flowering. J. Ecol. 106: 126–136.

McMahon, S. M., and J. M. Diez. 2007. Scales of association: Hierarchical linear models and the measurement of ecological systems. Ecol. Lett. 10: 437–452.

Mendoza, I., G. Martin, A. Caubère, P. Châtelet, I. Hardy, I. Jouard, and P.-M. Forget. 2015. Does masting result in frugivore satiation? A test with *Manilkara* trees in French Guiana. J. Trop. Ecol. 2015: 553–556.

Mendoza, I., C. A. Peres, and L. P. C. Morellato. 2017. Continental-scale patterns and climatic drivers of fruiting phenology: A quantitative Neotropical review. Global Planet. Change 148: 227–241.

Mendoza, I., R. Condit, S. J. Wright, A. Caubère, P. Châtelet, I. Hardy, and P.-M. Forget. 2018. Data and code supporting "Inter-annual variability of fruit timing and quantity at Nouragues (French Guiana): insights from hierarchical Bayesian analyses". Zenodo Repository, https://doi.org/10.5281/zenodo.1235013.

Mo, F., J. Zhang, J. Wang, Z.-G. Cheng, G.-J. Sun, H.-X. Ren, X.-Z. Zhao, W. K. Cheruiyot, L. Kavagi, J.-Y. Wang, and Y.-C. Xiong. 2017. Phenological evidence from China to address rapid shifts in global flowering times with recent climate change. Agric. For. Meteorol. 246: 22–30.

Morellato, L. P. C., B. Alberton, S. T. Alvarado, B. Borges, E. Buisson, M. G. G. Camargo, L. F. Cancian, D. W. Carstensen, D. F. E. Escobar, P. T. P. Leite, I. Mendoza, N. M. W. B. Rocha, N. C. Soares, T. S. F. Silva, V. G. Staggemeier, A. S. Streher, B. C. Vargas, and C. A. Peres. 2016. Linking plant phenology to conservation biology. Biol. Conserv. 195: 60–72.

Morellato, L. P. C., M. G. G. Camargo, and E. Gressler. 2013. South and Central America: Phenology overview and perspectives. In M. D. Schwartz (Ed.). Phenology: An integrative environmental science, pp. 91–113. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Newstrom, L. E., G. W. Frankie, and H. G. Baker. 1994. A new classification for plant phenology based on flowering patterns in lowland tropical rain-forest trees at La Selva, Costa Rica. Biotropica 26: 141–159.

Norden, N., J. Chave, P. Belbenoit, A. Caubere, P. Chatelet, P.-M. Forget, and C. Thebaud. 2007a. Mast fruiting is a frequent strategy in woody species of eastern South America. PLoS ONE 2: e1079.

Norden, N., J. Chave, A. Caubère, P. Châtelet, N. Ferroni, P.-M. Forget, and C. Thébaud. 2007b. Is temporal variation of seedling communities determined by environment or by seed arrival? A test in a neotropical forest. J. Ecol. 95: 507–516.

Numata, S., M. Yasuda, R. O. Suzuki, T. Hosaka, N. S. M. Noor, C. D. Fletcher, and M. Hashim. 2013. Geographical pattern and environmental correlates of regional-scale general flowering in Peninsular Malaysia. PLoS ONE 8: e79095.

Pearse, W. D., C. C. Davis, D. W. Inouye, R. B. Primack, and T. J. Davies. 2017. A statistical estimator for determining the limits of contemporary and historic phenology. Nat. Ecol. Evol. 1: 1876–1882.

Peres, C. A. 1994. Primate responses to phenological changes in an Amazonian terra-firme forest. Biotropica 26: 98–112.

Poncy, O., D. Sabatier, M. F. Prévost, and I. Hardy. 2001. The lowland high rainforest: Structure and tree species diversity. In F. Bongers, P. Charles-Dominique, P.-M. Forget, and M. Théry (Eds.). Nouragues: Dynamics and plant animal interactions in a neotropical rainforest, pp. 31–46. Kluwer, Boston, Massachusetts.

R Development Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ratiarison, S., and P. M. Forget. 2013. The role of frugivores in determining seed removal and dispersal in the Neotropical nutmeg. Trop. Conserv. Sci. 6: 690–704.

van Roosmalen, M. G. M. 1985. Fruits of the Guiana flora. Institute of Systematic Botany, Utrecht University, Wageningen, The Netherlands.

Sabatier, D. 1985. Saisonnalité et déterminisme du pic de fructification en fôret guyanaise. Rev. Écol. (Terre Vie) 40: 289–320.

Sabatier, D., and H. Puig. 1986. Phénologie et saisonnalité de la floraison et de la fructification en forêt dense guyanaise. Mémoires du Muséum Nacional d'Histoire Naturelle Sér. A. Zool. 132: 173–184.

Sakai, S., R. D. Harrison, K. Momose, K. Kuraji, H. Nagamasu, T. Yasunari, L. Chong, and T. Nakashizuka. 2006. Irregular droughts trigger mass flowering in aseasonal tropical forests in Asia. Am. J. Bot. 93: 1134–1139.

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.

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 evolution of fruiting seasons in tropical forest. Oikos 15: 274–281.

Staggemeier, V. G., E. Cazetta, and L. P. C. Morellato. 2017. Hyperdominance in fruit production in the Brazilian Atlantic rain forest: The functional role of plants in sustaining frugivores. Biotropica 49: 71–82.

ter Steege, H., and C. A. Persaud. 1991. The phenology of a Guyanese timber species – A compilation of a century of observations. Vegetatio 95: 177–198.

Terborgh, J. 1983. The study site: Its climate and vegetation. In J. W. Terborgh (Ed.). Monographs in behavior and ecology. Five new world primates. A study in comparative ecology, pp. 8–24. Princeton University Press, Princeton, New Jersey.

Thomas, R. 1999. Forest productivity and resource availability in lowland tropical forests of Guyana. PhD dissertation. Imperial College. University of London, London, UK.

Visser, M. E., S. P. Caro, K. van Oers, S. V. Schaper, and B. Helm. 2010. Phenology, seasonal timing and circannual rhythms: Towards a unified framework. Philos. Trans. R. Soc. Lond Ser. B: Biol. Sci. 365: 3113–3127.

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

Wright, S. J., and C. P. van Schaik. 1994. Light and the phenology of tropical trees. Am. Nat. 143: 192–199.

Zhang, S.-Y., and L.-X. Wang. 1995. Comparison of three fruit census methods in French Guiana. J. Trop. Ecol. 11: 281–294.

Zimmerman, J. K., S. J. Wright, O. Calderón, M. A. Pagan, and S. Paton. 2007. Flowering and fruiting phenologies of seasonal and aseasonal neotropical forests: The role of annual changes in irradiance. J. Trop. Ecol. 23: 231–251.