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A phenology model for tropical species that flower multiple times each year

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Abstract

Phenology models developed for temperate and boreal plants predict a single, population-level first flowering date for each year. These models cannot accommodate species that flower multiple times each year in humid tropical forests nor flowering data with census-interval rather than daily temporal resolution. Here, we present a new model framework able to predict the timing of multiple annual flowering events from census data. We extend a recent model, which predicted tropical flowering probabilities as discrete events occurring on census dates, by integrating predicted flowering probabilities over all dates between censuses. We evaluate our model against 29 years of daily climate and weekly flowering records for *Hybanthus prunifolius* (Violaceae) and *Handroanthus guayacan* (Bignoniaceae) from Barro Colorado Island, Panama. Previous experiments demonstrate that both species flower shortly after a heavy, dry-season rain interrupts an extended dry period. Our model captures this sequence of rainfall events. Best-fit model parameters are consistent with previous experimental results. This match suggests the new model framework will provide novel insights for other humid tropical forest species.

KEYWORDS

Barro Colorado Island, drought, proximate cue, rain flower, tropical forest

1 | INTRODUCTION

Seasons are an inevitable consequence of Earth's obliquity, and organisms everywhere have evolved mechanisms to time key life history events to appropriate seasons. At temperate and boreal latitudes, plants use photoperiod, winter vernalization and growing degree-days as proximate cues to synchronize flowering and other activities with favorable environmental conditions. These insights come from experiments with model organisms and from phenology models that use environmental variables to predict timing for species that are difficult to manipulate experimentally. These models share two properties appropriate for plants subjected to temperate and boreal climates (reviewed by Chuine & Régnierè, 2017). First, in most models, winter dormancy begins on a fixed date. Second, all models predict a single first flowering date for each year. Model validation involves comparisons of predicted first flowering dates with observed, population-level first flowering dates. These models show great promise where winter enforces dormancy, species flower just once each year and population-level first flowering dates are available.

Humid tropical forests violate all three conditions (Abernethy, Bush, Forget, Mendoza, & Morellato, 2018). First, the growing season never ends. A drier season might constrain epiphytes and plants with shallow root systems, but most tree and liana species are evergreen and stand-level

photosynthesis occurs at similar levels year-round (Restrepo-Coupe et al., 2013). Second, many humid tropical forest species flower multiple times each year (Newstrom, Frankie, & Baker, 1994; Zimmerman, Wright, Calderon, Pagan, & Paton, 2007). Third, the exact population-level first flowering dates that motivated the development of phenology models for crops, orchards and abundant native species of temperate and boreal plants (Chuine & Régnierè, 2017) are unavailable for humid tropical forests. Here, there are hundreds to thousands of plant species, the most abundant species comprise just a few percent of all individuals and reproductive adults are even rarer. For these reasons, tropical forest phenology data come from censuses of focal plants or of plant organs fallen onto ground transects or into litter traps (Mendoza, Peres, & Morellato, 2017). These censuses occur weekly, biweekly or monthly, and these census intervals limit temporal resolution. The exact day of first flowering is unknown because modest numbers of individuals of any one species are observed at multi-day intervals.

Here, we develop a phenology model appropriate to these realities. We begin with the modeling approach of Chen et al. (2018). Chen et al. (2018) model flowering probabilities on discrete dates corresponding to censuses. In contrast, we model the probability that the environmental signal for flowering is realized for every possible date and integrate these probabilities over dates between censuses. We evaluate our model for two humid tropical forest species for which prior experiments identified proximate flowering cues. This presents a rare opportunity to validate our approach by exploring the match between proximate cues determined experimentally and proximate cues inferred through modeled relationships between environmental variables and flowering events. We use daily climate records to predict flowering times and 29 years of weekly flowering records obtained from litter traps to validate our predictions. Arrival in litter traps closely represents flowering times in humid, lowland tropical forests because individual flowers last a single day in most species (Primack, 1985) even though a given plant might flower for weeks. We will consider our modeling framework to be successful if best-fit model parameters match experimentally determined flowering cues.

2 | METHODS

2.1 | Study site and species

Our study took place on Barro Colorado Island (BCI), Panama (9°9′ N, 79°51′ W). BCI supports tropical moist forest in the Holdridge Life Zone System (Croat, 1978). Annual rainfall averages 2,600 mm, with just 10% falling during a 4-month dry season (December–April). Temperatures average 26°C for 11 months and 27°C in April (Windsor, 1990). Leigh Jr (1999) provides further descriptions of BCI.

Our study species are *Hybanthus prunifolius* (Humb. & Bonpl. ex Schult.) Schulze-Menz (Violaceae) and

Handroanthus guayacan (Seem.) S.O.Grose (Bignoniaceae). Henceforth, we will refer to them by genus only. On BCI, *Hybanthus* is an abundant understory shrub and *Handroanthus* is a common canopy tree (Croat, 1978). Both species flower several times between January and May in most years (Croat, 1978, Augspurger, 1982, this study).

Augspurger (1980, 1981, 1982) combined 9 years of observations and two experiments to establish proximate flowering cues for *Hybanthus*. During the 9 years of observations, flowering never occurred unless it rained several days earlier, and major flowering events never occurred before 11 February. The first experiment established that flowering requires prior drought. Twenty individuals watered regularly throughout the dry season did not flower. The second experiment explored the duration of drought required before flowering during a dry season that began on 28 December. A single, saturating application of water failed to stimulate flowering before 4 February and stimulated minor and major flowering responses after 4 and 27 February, respectively. Thus, even minor flowering responses require at least 39 days of prior dry conditions. In addition, the mean delay between rainfall (or irrigation) and the onset of flowering varied from 8–11 days among years and experiments. We will attempt to infer the duration of the prior dry period and the duration of the delay between rain and flowering documented experimentally by Augspurger (1982) and also the amounts of rain consistent with dry conditions and required to stimulate flowering using a model comparison framework and 29 years of daily rainfall and weekly flowering records.

Gentry (1976) described "big bang" flowering stimulated by dry-season rain events in four *Tabebuia* species, two of which are now in the genus *Handroanthus* including *H. guayacan* (Grose & Olmstead, 2007). A single, saturating application of water during the dry-season stimulated flowering in three of these species (Borchert, 1994; Reich & Borchert, 1982). Experimental irrigation that prevented soil drying prevented dry-season flowering of *H. guayacan* on BCI (Wright & Cornejo, 1990a; Wright & Cornejo, 1990b). Control individuals were dry-season deciduous and flowered after a dry-season rain. Irrigated individuals retained their leaves throughout the dry season and flowered asynchronously during the following wet season when different major branches within the same tree abscised their leaves and flowered at different times. Although these experiments lack the detail available for *Hybanthus*, they confirm that normal flowering requires dry-season drought followed by a rainfall event. We will attempt to quantify these requirements.

2.2 | Rainfall and flower data

Rainfall was measured manually with a rain gauge (Novalynx 26-2,510, Auburn, CA) in the laboratory clearing on BCI and electronically with a tipping bucket (Li-Cor 1,400-106, Lincoln, NE) mounted above the forest canopy

on a nearby tower. We used manual daily rainfall when available, filling gaps with prorated tipping bucket values. For further documentation, see https://repository.si.edu/handle/10088/29560 (doi: 10.5479/data.stri/10088/29560).

We censused flowers captured in 200 litter traps each week from February 3, 1987 through December 27, 2016, identifying each flower to species. We recorded species-level flower presence because flowers are far too numerous to count for most species. Each census took 2 or 3 days to complete, with different traps censused on different days. Traps were located at 13.5-m intervals on alternating sides and 4–10 m from pre-existing trails within a 50-ha Forest Dynamics Plot (FDP). Each trap had a surface area of 0.5 m^2 composed of a loose, 1-mm mesh bag of plastic-coated fiberglass window screen suspended 0.8–1 m above the ground from a frame constructed of polyvinyl chloride pipe (PVC). *Hybanthus* can flower with a diameter at breast height (DBH) of just 8 mm (SJ Wright, personal observation). The species-specific allometric relationship between height and DBH gives an expected height of 2.3 m for *Hybanthus* at this DBH, which is well above our traps (Martínez Cano, Muller-Landau, Wright, Bohlman, & Pacala, unpublished data). Wright and Calderón (1995) provide further details.

For each census, we calculated the number of relevant traps with flowers present and absent and a mean census date with traps weighted equally. Relevant traps have a reasonable chance of capturing flowers of a species and are necessary because most species are rare in tropical forests. For example, 75% of the 314 tree and shrub species present have less than one reproductively sized individual per hectare in the 50-ha FDP and most traps are too distant from a reproductive individual of any particular species to capture its flowers. For large tree species, we identified relevant traps by proximity to potentially reproductive individuals (Chen et al., 2018), which are larger than 300 mm in DBH in *Handroanthus* (Robin Foster, unpublished data; Visser et al., 2016). Censuses of the 50-ha FDP provided locations and DBH of every tree at 5-year intervals between 1985 and 2015. We assumed deaths occurred midway between censuses and interpolated DBH linearly between censuses for survivors to identify trees present each year and estimate their size. We then examined the cumulative distribution of distances between traps that captured flowers and the nearest reproductively sized adult for each year and selected the distance that accounted for 80% of flower presences over the 29-year record. This distance was 19.8 m for *Handroanthus* (Figure S1, Supporting Information). We could not use this protocol for *Hybanthus* because flowering can occur before the 10-mm DBH threshold for inclusion in FDP censuses and an unknown number of reproductive individuals are undocumented. Instead, we identified relevant traps for each calendar year to be the traps that captured *Hybanthus* flowers at least once during the year. This allows us to

distinguish minor and major flowering events within years but not between years.

2.3 | Model and analysis

Our model for the probability that a trap captures flowers in a given census involves sub-models for the drought precondition, for the rainfall cue, and for a lag between the date these conditions are fulfilled and the date flowers appear. The environmental conditions associated with the rainfall cue and the drought precondition involve the accumulation of rainfall over multiple days, and the comparison of mean daily rainfall with thresholds.

We define $R(d)$ as the rainfall on date d in mm. We model the rainfall cue $e_R(d)$ on date d as a logistic function (with slope β_R) of the amount by which mean daily rainfall over the preceding τ_R days exceeds a threshold α_R (Figure 1b). Specifically,

$$e_R(d) = \frac{1}{1 + \exp\left(-\beta_R\left(\frac{1}{\tau_R}\sum_{d-\tau_R}^{d} R(d) - \alpha_R\right)\right)} \quad (1)$$

Our model for the drought precondition takes a similar form. We model the drought signal $e_{D1}(d)$ for date d, τ_R and $R(d)$ as a logistic function (with slope β_D) of the amount by which mean daily rainfall over the preceding τ_D days falls below a threshold α_D (Figure 1c). Specifically,

$$e_{D1}(d) = \frac{1}{1 + \exp\left(-\beta_D\left(\alpha_D - \frac{1}{\tau_D}\sum_{d-\tau_R-\tau_D}^{d-\tau_R} R(d)\right)\right)} \quad (2a)$$

As α_D becomes very small, the maximum value of $e_{D1}(d)$ is less than one in Equation (2a), which precludes a strong drought signal (Figure S2). To avoid this problem, we also used log-transformed rainfall. The alternative formulation based on log-transformed mean rainfall is

$$e_{D2}(d) = \frac{1}{1 + \exp\left(-\beta_D\left(\log(\alpha_D) - \log\left(\frac{1}{\tau_D}\sum_{d-\tau_R-\tau_D}^{d-\tau_R} R(d)\right)\right)\right)} \quad (2b)$$

Note that zero and one bound all three environmental condition functions.

Phenological events always lag their environmental cues, reflecting the time for organisms to organize responses (e.g., Augspurger, 1982; Borchert, 1994; Reich & Borchert, 1984; Yeoh et al., 2017). In the case of litter trap observations of flowering, there can be an additional lag from flowering to the time fallen flowers are recorded in traps if abscised flowers fail to detach immediately or become suspended on lower vegetation. We model the distribution of lag times t with a truncated normal or
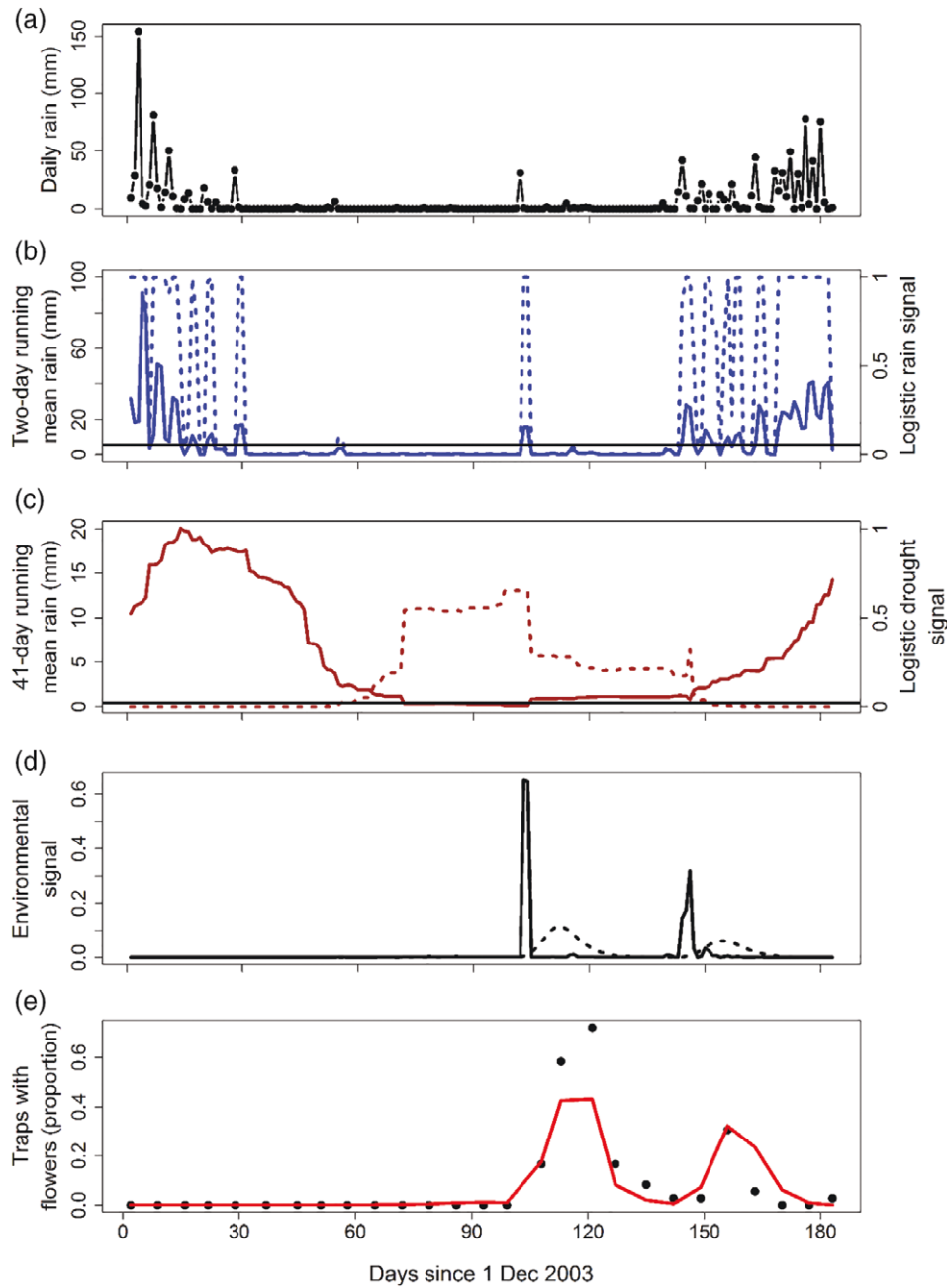
FIGURE 1 The model illustrated for rainfall and *Hybanthus* flower observations from December 1, 2003 through May 31, 2004. Panel a presents daily rainfall. Panel b presents 2-day running mean rainfall (solid blue line), where 2 days is the best-fit value for the duration of the rainfall cue, the logistic rainfall signal (dashed blue line, see Equation (1)) and the best-fit value for the threshold level of rainfall that is an effective cue (α_R, horizontal black line). Panel c presents 41-day running mean rainfall (solid brown line), where 41 days is the best-fit value for the duration of required drought, the logistic drought signal (dashed brown line, see Equation (2a)) and the best-fit value for the threshold level of rainfall that constitutes drought (α_D, horizontal black line). Panel d presents the environmental signal as the product of the logistic rainfall and logistic drought signals (solid line) and after incorporating the best-fit lag between the rainfall cue and flower observations (dashed line, see Equation (3)). Panels a through d present daily values. Panel e presents predicted (red line, see Equation (4)) and observed (black circles) proportions of traps with flowers for 27 censuses

truncated skew-normal distribution, *g(t)*. We tried the skew normal distribution because it captures a long tail of delayed observations that characterizes flower presences in litter traps for many BCI species (SJ Wright, unpublished analysis). We truncated both distributions t_{max} days after each day's environmental cue to simplify computations. We arbitrarily set $t_{max} = 70$ days, which turned out to be appropriate (see Section 3).

Combining the environmental conditions and the lag time distribution gives the probability $p_{day}(d)$ that flowers fall on a given day *d* (Figure 1d):

$$p_{day}(d) = \sum_{t=-t_{max}}^{0} e_R(d+t)e_D(d+t)g(t) \qquad (3)$$

We calculated the total probability flowers fell into a trap during census *c* under the assumption that flower fall on

different days is independent. Thus, the probability of not catching any flowers in a census is the product of the probabilities of not catching flowers on all days in that census, and the probability of catching flowers is one minus this (Figure 1e):

$$p_{census}(c) = 1 - \prod_{d=D_{mn}(c-1)+1}^{d=D_{mn}(c)} (1 - p_{day}(d)) \quad (4)$$

where $D_{mn}(c)$ is the mean date of census c.

The total log likelihood (*LL*) of the data is then

$$LL = \sum_c \left[N_p(c) \log(p_{census}(c)) + N_a(c) \log(1 - p_{census}(c)) \right]$$

where $N_p(c)$ and $N_a(c)$ are the numbers of relevant traps with flowers present and absent in census c, respectively.

Table 1 summarizes definitions of all parameters, variables, and functions, as well as constraints on parameter values. Two parameters, τ_R and τ_D, take only integer values. Biological constraints include positive logistic slopes (Equation (3)), positive mean lags (μ) between flowering and its environmental signal, and bounds on threshold daily rainfall at 5 mm/day, which approximates evapotranspiration on BCI. In addition, we placed upper and lower bounds on the number of days over which rainfall is integrated for the drought precondition and rainfall cues based on past

observations. We bounded τ_R at 1–4 days and τ_D at 15 through 45 days for *Handroanthus* and 25 through 55 days for *Hybanthus*. We placed these bounds in part for computational convenience because τ_R and τ_D are integer valued, which precluded their optimization under standard algorithms. The chosen bounds include the full range of biologically reasonable values (Augspurger, 1982; Borchert, 1994; Reich & Borchert, 1984; Wright & Cornejo, 1990a, 1990b; SJ Wright, personal observations), and model fits deteriorated rapidly for $\tau_R > 2$ and for τ_D within 8 days of either bound.

We searched for the maximum likelihood for each pairwise combination of the allowed integer values of τ_R and τ_D, and then took the overall maximum as the maximum likelihood model. We used the default Nelder–Mead method and the constrained optimization command ("constrOptim") in R 3.3.2 (Core Team, 2016) and the skew normal R package (Azzalini, 2017) to maximize *LL*. To avoid local maxima, we performed 20 optimizations for each combination of τ_R and τ_D with initial values of the remaining parameters drawn from random uniform distributions. For each species, we compared four models with linear (Equation (2a)) or logarithmic (Equation (2b)) drought signals and with normal or skew normal lag distributions. For each model, we

TABLE 1 Variables, model parameters and fitted functions, with their definitions and constraints

	Symbol	Definition (units)	Constraint (rationale)
Variables	d	Date (day)	Integer
	c	Census number	Integer
	t	Time lag between cue date and flower fall (days)	Integer
Observed data	$R(d)$	Rainfall on date d (mm)	
	$D_{mn}(c)$	Mean date of census c (day, rounded)	Integer
	$N_p(c)$	Number of relevant traps with flowers in census c	Integer, 0 to 200
	$N_a(c)$	Number of relevant traps without flowers in census c	Integer, 0 to 200
Drought precondition (Equations (2a), (2b), and (3))	τ_D	Parameter for duration of drought (days)	Integers 25 to 55 for *Hybanthus* (past observations)
	α_D	Parameter for daily rainfall threshold for drought (mm/day)	0 to 5 (daily evapotranspiration $\approx$ 5 mm/day)
	β_D	Parameter for logistic slope for drought response	Positive (see Equation (3))
	$e_D(d)$	Fitted function for environmental signal for drought response on date d (logistic function)	
Rainfall Cue (Equations (1) and (3))	τ_R	Parameter for duration of rain cue (days)	Integers 1 to 4 (past observations)
	α_R	Parameter for daily rainfall threshold for rain cue (mm/day)	>5 (daily evapotranspiration $\approx$ 5 mm/day)
	β_R	Parameter for logistic slope for rainfall response	Positive (see Equation (3))
	$e_R(d)$	Fitted function for environmental signal for rainfall response on date d (logistic)	
Lag (general)	μ	Parameter for mean lag (days)	Positive
	σ	Parameter for SD of lag (days)	Positive
	γ	Parameter for skewness of lag (days)	
	t_{max}	Fixed constant for maximum number of days that lag function is integrated	70
	$g(t)$	Fitted probability distribution of time lag t between cue date and date fallen flowers are recorded	Normal or skew normal truncated at t_{max} days
Integrative functions	$p_{day}(d)$	Probability flowers fell into a trap on date d	
	$p_{census}(c)$	Probability flowers fell into a trap during census c	

TABLE 2 Model performance indices and estimated parameter values for best-fit models

Species		Handroanthus guayacan				Hybanthus prunifolius			
Lag		Normal		Skew normal		Normal		Skew normal	
Drought signal		Linear	Log	Linear	Log	Linear	Log	Linear	Log
Drought precondition parameters	τ_D	22	31	22	31	41	41	41	42
	α_D	1.8e-6	0.668	5.0e-7	0.637	0.408	0.553	0.410	0.543
	β_D	1.77	2.63	1.78	2.55	1.97	2.72	1.98	2.67
Rainfall cue parameters	τ_R	2	1	2	1	2	2	2	2
	α_R	9.23	16.3	9.38	16.3	5.60	5.99	5.57	5.96
	β_R	0.440	0.283	0.425	0.278	1.06	1.03	1.07	1.02
Lag distribution parameters	μ	2.92	5.32	12.3	12.6	10.2	10.7	10.5	10.9
	σ	13.2	12.3	7.89	7.58	4.84	4.71	4.73	4.65
	γ	—	—	0.964	0.970	—	—	0.484	0.556
Performance indices	AIC	4,014	4,064	**4,004**	4,050	9,160	9,212	**9,148**	9,204
	RMSE	0.0639	0.0634	0.0633	**0.0625**	0.0845	0.0833	0.0844	**0.0832**
	EFF	0.353	0.364	0.365	**0.381**	0.564	0.576	0.565	**0.578**

Note. The four combinations of lag (second row) and drought signal (third row) define four models for each species. The two lags refer to normal and skew normal distributions of lag times between flower fall and its environmental cues. We report the mean (μ), SD (σ) and, for the skew normal distribution, the skewness (γ) of the fitted lag distributions. The two drought signals scale drought linearly and logarithmically (Equation (2a) and (2b)). Bolding highlights best-fit models for each performance index. AIC: Akaike Information Criterion; EFF: efficiency; RMSE: root mean square error.

calculated three performance measures: the Akaike Information Criterion (AIC), root mean square error (RMSE) and efficiency (EFF) as follows:

$$\text{AIC} = 2k - 2LL,$$

where k is the number of parameters. Models with normal and skew normal lag distributions have eight and nine parameters, respectively (Table 2).

$$\text{RMSE} = \frac{1}{n}\sqrt{\sum_{c=1}^{n}(O(c) - p_{census}(c))^2}$$

where $O(c)$ is the observed proportion of traps with flowers in census c ($O(c) = N_p(c)/(N_p(c) + N_a(c))$) and n is the number of censuses.

$$\text{EFF} = 1 - \frac{\sum_{c=1}^{n}(O(c) - p_{census}(c))^2}{\sum_{c=1}^{n}\left(O(c) - \overline{O}\right)^2}$$

where $\overline{O}$ is the mean value of $O(c)$. EFF is the most general definition of the coefficient of determination, and can be interpreted similarly to an r^2 value.

3 | RESULTS

We conducted 1,505 weekly censuses of 200 traps between February 3, 1987 and December 29, 2015 and recorded *Handroanthus* flowers 647 times in 42 unique traps and *Hybanthus* flowers 1,859 times in 129 unique traps. We recorded one to three flowering events for both species in each of the 29 dry seasons, with the single exception of zero *Handroanthus* flowers recorded in 1988 (Figures 2 and 3).

Models with skew normal lag time distributions outperformed models with normal lag time distributions for both species and both drought signals (Table 2). Models with linearly scaled drought signals (Equation (2a)) and skew normal lag time distributions minimized *AIC* for both species (Table 2). The best-fit estimates for the lag time and its *SD* were 12.3 ± 7.9 and 10.5 ± 4.73 days for *Handroanthus* and *Hybanthus*, respectively (Table 2). With these values, the 70-day limit in Equation (3) excludes a trivial tail of the lag time distribution.

For *Hybanthus*, the best-fit model by *AIC* explained 56.5% of the variation in flowering intensity among censuses (see EFF in Table 2). The model predicted flowering events that did not occur in 1991 and 2003, and severely under predicted early dry season flowering events in 1996, 2008, 2009 and 2014 (Figure 2). Still, the best-fit model predicted the timing of most flowering events reasonably well (Figure 2). The best-fit parameter values also aligned well with experimentally determined values (Table 2). The inflection point for the logistic drought signal (Equation (2a)) occurs after 41 dry days averaging just 0.41 mm of rain per day. Augspurger (1982) determined experimentally that flowering requires at least 39 prior dry days. The mean lag between flower fall and its cue is 10.5 days. Flowers first fall 1 day after opening (SJ Wright, personal observation), so we should reduce this mean lag by 1 day to compare with the mean lag of 8–11 days determined experimentally by Augspurger (1982). The inflection point for the logistic rainfall cue (Equation (1)) occurs after two rainy days averaging 5.6 mm of rain per day.

For *Handroanthus*, the best-fit model by *AIC* was less successful, explaining 36.5% of the variation in flowering intensity among censuses (Figure 3, see EFF in Table 2).
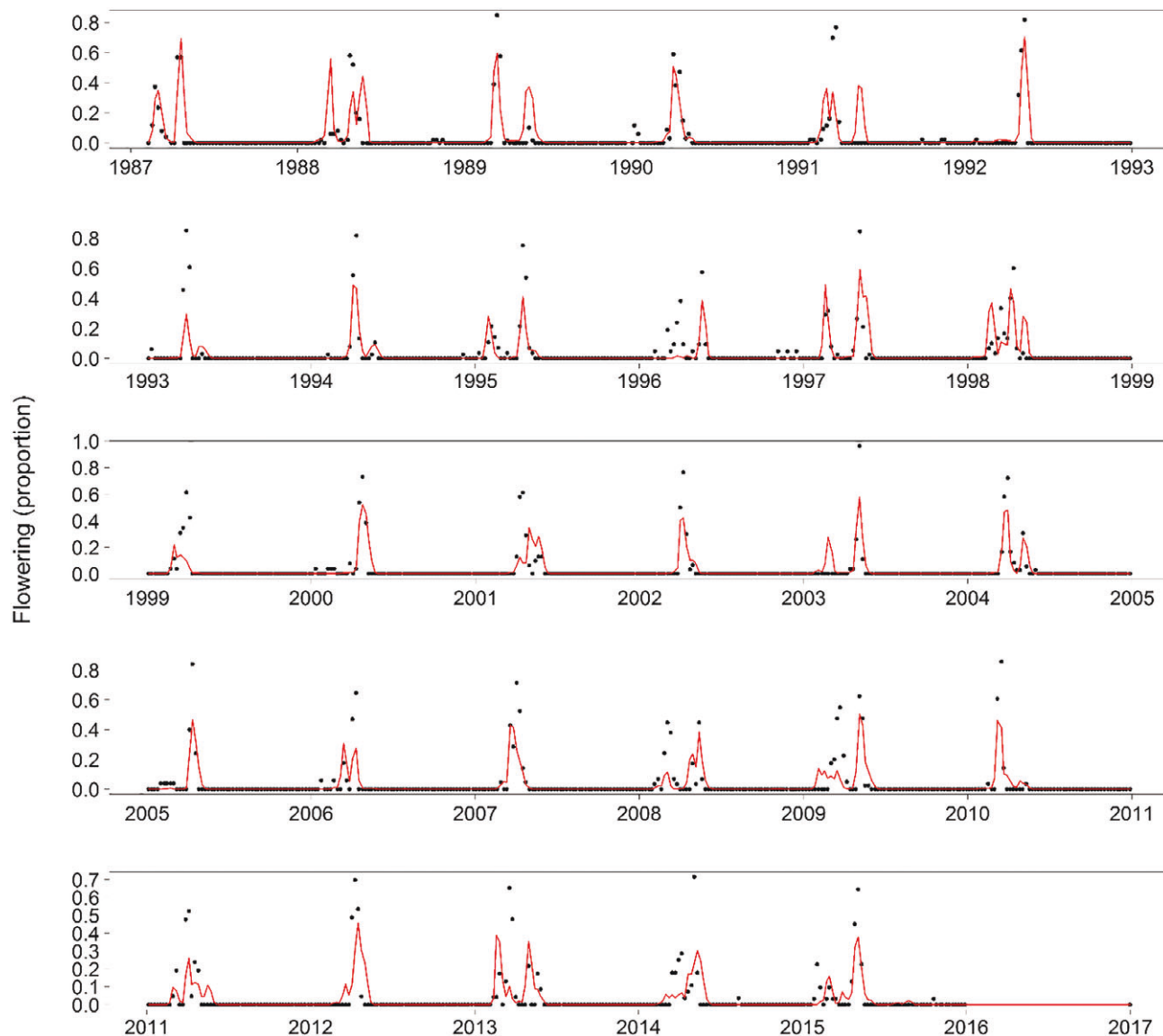
FIGURE 2 The observed proportion of relevant traps that captured *Hybanthus* flowers (black circles) in 1,505 weekly censuses of 200 traps conducted on Barro Colorado Island, Panama. The red line is the predicted proportion for the best-fit model. Tick marks and years are located at 1 January

The model predicted flowering in 1988 when none occurred, and often predicted mid dry season flowering when none occurred. There was also a problematic parameter estimate. The inflection point for the linear drought signal (Equation (2a)) occurs after 22 bone-dry days averaging 0.0000005 mm of rain per day. Since rainfall cannot be negative, this constrains the logistic drought signal to values less than 0.5 (Figure S2). In addition, such extreme dry periods are rare on BCI (Windsor, 1990). For these reasons, we preferred the model with a logarithmic drought signal (Figure S2) despite its larger *AIC* value (Table 2).

4 | DISCUSSION

Previous phenology models predict population-level first dates for temperate and boreal plants (reviewed by Chuine & Régnière, 2017) or the probability of flowering on specific dates corresponding to censuses (Chen et al., 2018). We developed a new approach to phenology models appropriate for censuses of focal individuals (or fallen plant organs) that integrates predicted daily probabilities over the days between censuses. Rather than predict first dates, we predict the proportion of individuals, traps or transects showing evidence of a phenophase in each census. Our model is appropriate for phenological studies conducted in tropical forests where phenological data are for censuses not for exact dates, the great majority of plant species are rare, and censuses include modest numbers of focal individuals.

Our approach provided a reasonable match between predicted and observed flowering phenologies over 29 years for *Hybanthus prunifolius* (Figure 2). Best-fit model parameters also closely matched experimentally determined values (Augspurger, 1982) for the duration of dry conditions required before flowering (41 days vs. a minimum of 39 days, respectively) and for the mean duration of the lag
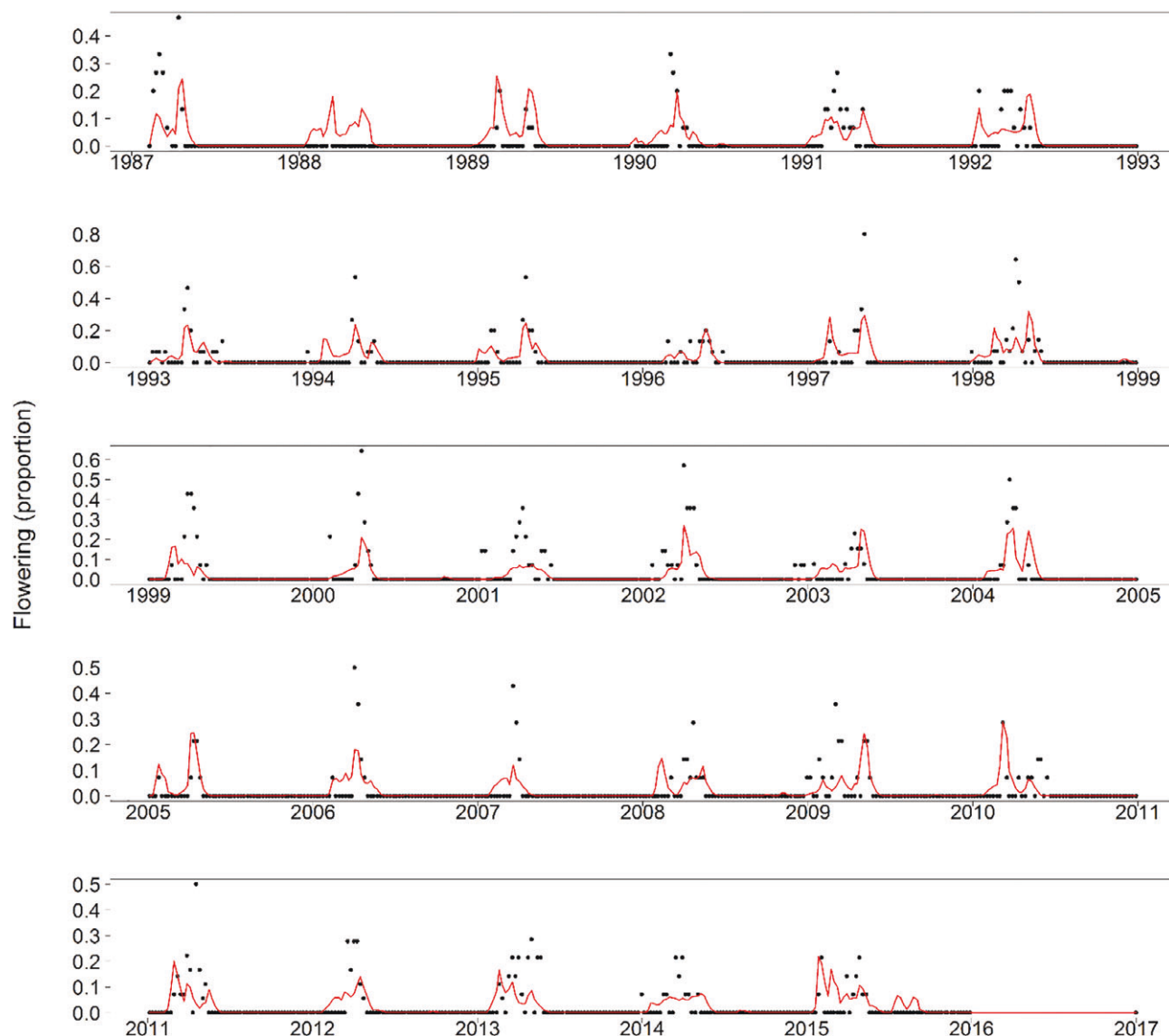
FIGURE 3 The observed proportion of relevant traps that captured *Handroanthus* flowers (black circles) in 1,505 weekly censuses of 200 traps conducted on Barro Colorado Island, Panama. The red line is the predicted proportion for the best-fit model. Tick marks and years are located at 1 January

between flowering and its environmental cue (10.5 days vs. 8–11 days, respectively). Best-fit model parameters also provided new insights into the levels of rainfall necessary to fulfill the requirement for prior dry conditions (0.41 mm rain per day over 41 days) and to initiate flowering (5.6 mm per day over 2 days). We note that the model of Chen et al. (2018) will fail to detect 2-day rainfall cues that fall between census dates.

Our approach did less well for *Handroanthus guayacan* (Figure 3 and Figure S3). We believe this reflects a limitation imposed by short intervals between massive flowering events and our weekly censuses of fallen flowers. This species has a "big bang" flowering phenology characterized by extreme synchrony within and among individuals (Gentry, 1976). In each flowering event, individuals bear flowers for 3 days only, and the overwhelming majority of individuals bear flowers for the same 3 or 4 days (Gentry, 1976; SJ Wright, personal observation). Experiments demonstrate that

this species requires prior dry conditions to flower (Wright & Cornejo, 1990a, 1990b). Best-fit estimates are 22 days for the duration of dry conditions, 12.3 days for the mean lag between flowering and its rainfall cue and 7.9 days for the *SD* of the lag (Table 2). We believe the large variation around the mean lag is an artifact of censuses of the presence/absence of fallen flowers, the immense numbers of flowers produced, and the potential to flower at relatively short intervals of 22 days. A long tail of flower trap presences is inevitable if even minute percentages of flowers abscise but do not fall to the ground immediately. Flower trap presences from different flowering events overlap, obscuring discrete flowering events. Fortunately, overlap between flowering events will rarely be a problem for other species because most humid tropical forest species flower at intervals substantially longer than 22 days (e.g., Chen et al., 2018; Newstrom et al., 1994; Numata et al., 2013; Sakai et al., 2006; Zimmerman et al., 2007).

Our next steps will be to refine and apply our model to additional species. Many refinements are possible. As just one example, for *Hybanthus* the lag between rainfall and flowering decreases and flowering synchrony increases with the amount of rain that interrupts dry conditions (Augspurger, 1982). We could model the parameters used to describe the lag time distribution as functions of $\sum_{d-\tau_R}^{d} R(d)$ (Equation (1)) to incorporate this observation into a new, refined model. Additional models might be tailored to capture other hypothesized environmental cues or to the natural history of specific species and sites.

Our model captures the following temporal sequence of environmental cues and phenological responses:

1. a constraint imposed by unfavorable environmental conditions (in our case drought),
2. a return to favorable environmental conditions (in our case rain) that initiates a phenological event (in our case flowering), and
3. a lag between the return of favorable conditions and the realization of the phenological event.

This temporal sequence describes two of the leading hypotheses advanced to explain plant phenology in humid tropical forests. The hypotheses are that renewed growth (usually leaf production and/or flowering) occurs after rainfall relieves drought (Reich & Borchert, 1984) or after seasonal increases in solar inputs relieve light limitation (van Schaik, Terborgh, & Wright, 1993; Wright & van Schaik, 1994; Yeang, 2007). We recently evaluated these hypotheses using a model developed for temperate zone plants that replaced the first step in this temporal sequence with a fixed date after which the arrival of favorable conditions initiated flowering (Wright & Calderón, 2018). This approach failed to identify a single BCI species that flowered in response to the arrival of rain (Wright & Calderón, 2018). Given our success here with *Hybanthus* (Figure 2), we will re-evaluate the relationship between flowering and rainfall for all BCI species.

There are increasing numbers of long-term phenology studies from tropical forests (e.g., Chen et al., 2018; Morellato, Abernethy, & Mendoza, 2018) including 18 seed trap studies using the CTFS-ForestGeo protocols used here (see Table S6 in Anderson-Teixeira et al., 2015). We hope our success and the success of Chen et al. (2018) will encourage others to use similar modeling approaches to evaluate hypothesized proximate cues with long-term tropical phenology data sets. Hypothesized proximate cues for tropical plant phenology include short temperature dips, seasonally sufficient moisture availability, prior drought followed by rain, levels of solar irradiance at the forest canopy, levels of solar insolation at the top of the atmosphere and photoperiod (reviewed by Wright & Calderón, 2018). The specific proximate cue—the required level and duration of the

environmental signal—is rarely, if ever known. As one example, Yeang (2007) wrote: "The specific attributes of high solar radiation that are critical to synchronous flowering still need to be determined: whether it is the average solar radiation received that is important or if it might be, for example, very high radiation on a few cloud free days, or the hours of high daily sunshine that are also relevant." Experiments to resolve specific environmental cues will rarely be possible for the large canopy trees and lianas that dominate humid tropical forests. Comparisons of predictions from models tailored to capture specific hypothesized environmental cues and long-term phenological and meteorological measurements are a promising route towards a quantitative understanding of the proximate cues for plant phenology in tropical forests.

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SUPPORTING INFORMATION

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

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