Tree Community Phenodynamics and Its Relationship with Climatic Conditions in a Lowland Tropical Rainforest

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Abstract: The timing, duration, magnitude and synchronicity of plant life cycles are fundamental aspects of community dynamics and ecosystem functioning, and information on phenodynamics is essential for accurate vegetation classification and modeling. Here, we recorded the vegetative and reproductive phenodynamics of 479 individuals belonging to 182 tree species monthly over two years in a lowland Atlantic Forest in southeastern Brazil, and assessed the relationship between local climatic conditions and the occurrence and intensity of phenophases. We found a constant but low intensity of occurrence of both leaf fall and leaf flush with respect to canopy cover, resulting in an evergreen cover throughout the year. The timing of the reproductive phenophases was irregular between the two years of observation, and their amplitude was low. In addition, flowering and fruiting phenograms of activity, intensity and intensity corrected by the basal area did not overlap. These results suggest that a combination of phenological records and community-structure parameters allows for the obtainment of more accurate estimates of resource availability over time. We found that differences in growing degree-days (GDD), photoperiod and precipitation over time were related to temporal variation in leaf fall, leaf flush and flowering, with a large consistency in responses across tree species in this lowland Atlantic Forest. Moreover, there was only a weak relationship between climatic conditions and the dynamics of fruit formation and ripening, which were more strongly related to flowering phenodynamics, which is suggestive of indirect effects of climatic conditions on fruiting. Finally, the association we found between the number of days with precipitation and leaf fall dynamics agrees with the view that the greater potential for extreme events may impair plant growth in tropical forests. This reinforces the growing concerns regarding the risk of ecological collapse of tropical forests due to fragmentation and global climate change.

Keywords: community ecology; climate change; global vegetation models; phenological intensity; tropical forest

1. Introduction

The timing, duration, magnitude and synchronicity of plant life cycles are fundamental aspects of community dynamics and ecosystem functioning [1]. Phenological data are among the most valuable indicators of ecological responses to climate change, as phenology is the natural aspect of simple

observation that responds most to climate change at several levels [2]. Global climate change has renewed the interest in the study of plant phenology, which is currently considered a multidisciplinary science that unites biometeorology, ecology and evolutionary biology [3]. Furthermore, phenological studies constitute the basis for understanding the dynamics of resource availability for populations of many animal species in tropical forests [4], and are important tools for biodiversity monitoring, management and conservation [5,6].

Although phenological studies have increased in recent decades [7] and great advances have come from the use of remote-sensing technologies and other methods [8], we simply do not have any systematic phenological information for most areas of Neotropical rainforests. There are still many gaps in our knowledge of how plant phenological events are regulated by climate in these environments, and methodological and analytical issues persist (e.g., [9,10]. For instance, many conclusions about the phenological patterns and their relationships with climatic conditions in tropical communities are based only on qualitative information (i.e., data on presence/absence of phenophases). However, qualitative measures of activity coupled with quantitative data on intensity are fundamental for more accurate definition of plant phenodynamics at the community and population levels [11,12]. Phenological studies that consider both the differences in crown size among individuals and density among species in tropical communities are even fewer (e.g., [13]).

Phenological events reflect both proximal and ultimate (or evolutionary) factors, and may also be influenced by phylogenetic conservatism [9,14,15]. Aspects of biotic interactions are commonly indicated as evolutionary pressures for current life-history strategies related to phenological patterns (i.e., ultimate factors), for example, plant competition for pollinators [16,17], avoidance of herbivory and seed predation [18,19], and more efficient seed dispersal [20]. In turn, environmental factors proximately interact with an organism's physiological and molecular mechanisms, determining the timing and magnitude of its phenological events. Some widely recognized proximate factors controlling the occurrence of plant phenophases are the local meteorological conditions, such as temporal variations in precipitation and temperature [21–23]. Yet, for most species little is known about the specific environmental factors and the underlying mechanisms that control the timing of phenological events [9], in particular for highly diverse tropical communities.

A broad understanding of the ultimate factors acting on the selection of phenological events in tropical forests is lacking, largely due to the challenges in distinguishing and measuring selective pressures in these complex environments. In contrast, changes of local climatic conditions may be more easily related to changes in phenological events, at both the population and community levels [24,25]. Accordingly, some degree of seasonality is often recorded for vegetative and reproductive phenophases in tropical forests at the community level, and the regulation of seasonality has been linked to oscillations in air temperature, photoperiod and precipitation [22,25,26] However, assessments of the phenodynamics based on community-structure parameters and its regulation by combined effects of proximate factors are still unresolved matters for tropical forests. As such, ground-based phenological data at the forest community level are important for statistical models of vegetation dynamics, by means of quantification of relationships with environmental descriptors (e.g., [26–28]).

We studied the vegetative and reproductive phenodynamics and their relationship with local climatic conditions in a remnant of lowland Atlantic Forest in southeastern Brazil. Our results add to the few phenological studies at the community level previously carried out in lowland Atlantic Forest [26,29] and will aid in establishing a better understanding of phenological patterns in this biodiversity hotspot. We used structural parameters of the community to characterize its phenodynamics, and we tested the association of phenological events with local climatic conditions to aid in evaluations of the impacts of climate change on phenological processes (see [30]). Our main aims were to determine: (1) how the activity and intensity of leaf phenophases determine the evergreen aspect of lowland forests; (2) how reproductive phenophases are distributed over time with respect to resource availability; (3) which differences in phenodynamics are observed at the community level

when structural parameters are considered; and (4) how are the phenodynamics of a lowland Atlantic Forest is related to variation in local climatic conditions.

2. Material and Methods

2.1. Study Area

This study was conducted in União Biological Reserve (Rebio União), a restricted nature reserve of Atlantic Forest located in the state of Rio de Janeiro (22°27′30″ S and 42°2′14″ W). The reserve was initially created for an area of ca. 2500 ha, but was recently expanded to cover 7756 ha (Figures S1 and S2). The topography is characterized by moderately dissected ridges with convex tops, which form a typical landscape of the Brazilian Eastern Basin (the so-called "Mares de Morros"), with a maximum elevation of 376 m [31]. Dystrophic red-yellow latosols predominate in the area [31], and the predominant vegetation at Rebio União is classified as lowland ombrophilous dense forest (sensu [32]) or lowland Atlantic Forest (sensu [33]). However, Rebio União borders the coastal region of Cabo Frio, a phytogeographical enclave characterized by xeric vegetation and semideciduous forests [34]. Due to this localization, there were doubts about the existence of some degree of deciduousness in Rebio União forests.

The regional climate is tropical wet-dry, with most precipitation occurring in the summer (Aw in the Köppen-Geiger-Pohl system). Data collection started in the 2000s at an automatic weather station located amongst the central facilities of the Rebio União, but there are several gaps that made it impossible to calculate the climate normal for this specific locality. Therefore, we compared available data from the Rebio União station to data from the nearby Macaé wheather station, located 20 km distant from our study site (22°24′14″ S and 41°51′33″ W, 32 m a.s.l.), and found no significant differences between the two. Hence, we gathered meteorological data from the Macaé weather station to calculate the last climate normal (from 1961 to 1990) and to perform all of our statistical analyses (see below). According to the last climate normal, the region has two distinct seasons: a dry season with lower temperatures between May and September; and, a wet season with higher temperatures between October and April; the mean annual precipitation is 1168.6 mm and the mean temperature is 24 °C (Figure 1A). The maximum photoperiod was 14.26 h/day in December and the minimum was 11.43 h/day in June (Figure 1B). Temperature and rainfall distribution in 2006 differed from the climate normal as well as from the distribution in 2007. Precipitation in the dry season was higher in 2006, as well as the amplitude between maximum and minimum temperatures (Figure 1C).
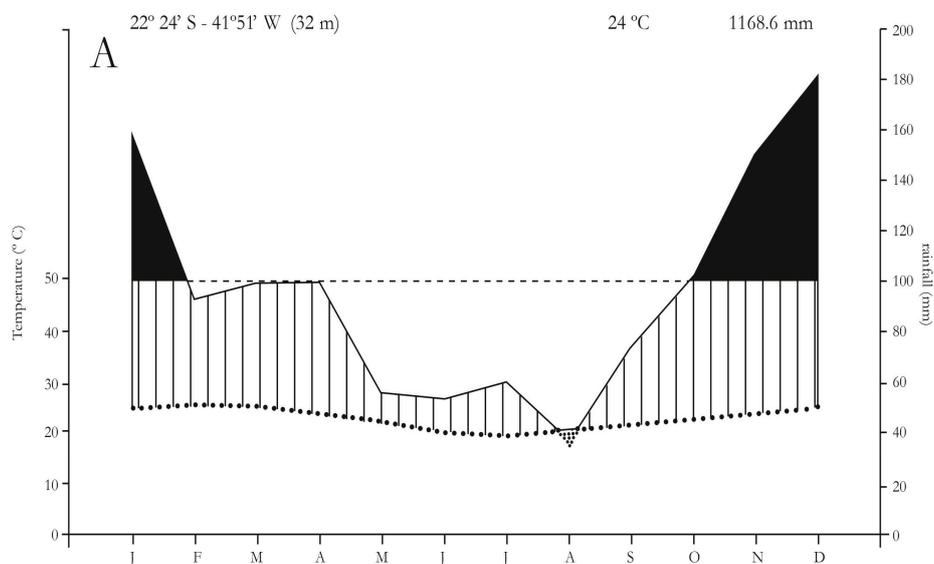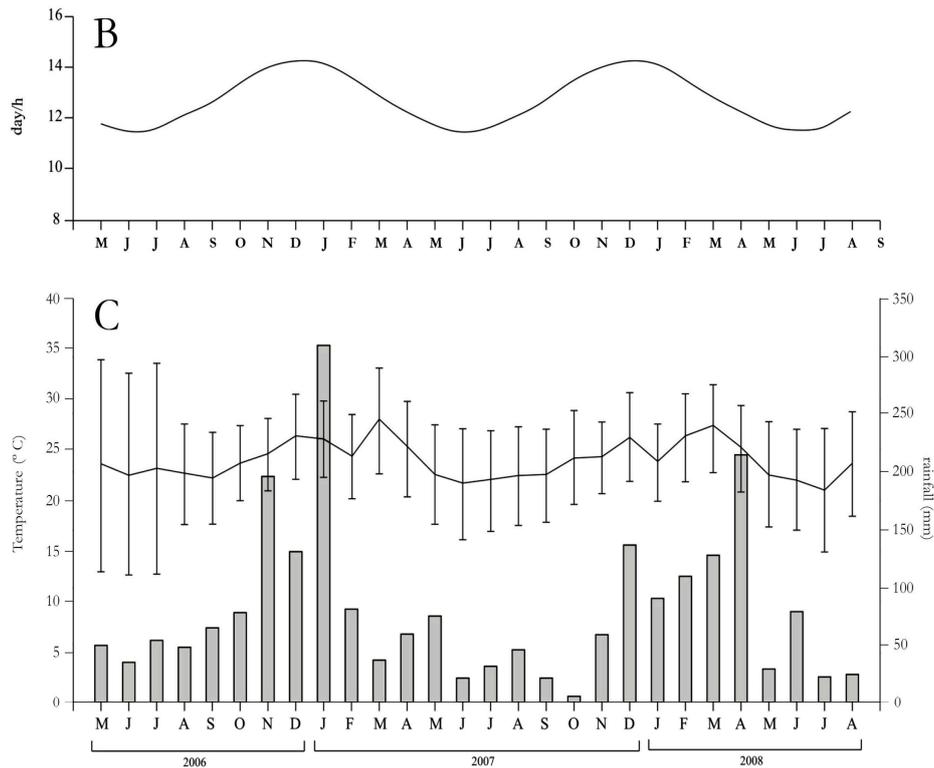

Figure 1. *Cont.*

Figure 1. Climate and meteorological patterns in the União Biological Reserve region, southeastern Brazil (data from the Macaé weather station). (**A**) Walter-Lieth climate diagram [1] of the last climate normal (1961–1990). The information above the panel corresponds to station location and altitude, the mean annual temperature, and the mean annual precipitation. Continuous and dotted lines indicate the monthly precipitation and mean temperature, respectively. The dotted area indicates dry period, the hatched areas indicate humid periods, and the black areas indicate wet periods; (**B**) Monthly photoperiod and (**C**) monthly total precipitation (gray bars) and mean, maximum, and minimum temperatures (line) for the study period (2006–2008).

2.2. Phenological Sampling

Sampling was carried out in nine permanent 20 m × 50 m plots established in the reserve in the 1990s (Figures S1 and S2), located in the forest interior and along the edges of clearings for a gas pipeline, about 25 m wide, and an electric transmission line, about 100 m wide (Figure S1). Data for phenological activity [12] and Fournier intensity [35] were collected monthly from August 2006 to August 2008 in each study plot. A total of 479 individual trees with diameter at breast height (DBH, 1.3 m aboveground) ≥ 10 cm, belonging to 182 species in 43 families (Table S1), were included in our study, and monitored monthly by the same observer (Jakeline P. A. Pires). This high number of species in our study plots is close to estimates of tree richness from a phytosociological inventory in the same area, which found 250 morphospecies of trees with DBH ≥ 10 cm in 1.2 ha, reaching 32 m² ha^{-1} of basal area [36].

The following vegetative and reproductive phenophases were recorded monthly for each marked individual from each species leaf fall, leaf flush, flowering, and fruiting (green and mature fruits). Leaf fall represents leaf deciduousness and was determined by observing the presence of fresh leaves on the ground and the presence of senescent leaves and gaps in the canopy. Leaf flush represents the emission of new leaves and was determined by the presence of young leaves (smaller and/or clear green or brownish) on the branches. Binoculars were used to observe the canopy of each tree, and the percentage of the phenophase over the whole canopy area was estimated, using the semi-quantitative method proposed by Fournier [35]. The Fournier intensity method scores each phenophase equal

to the magnitude of the event on a scale of 0–4, as follows: absent = 0; 1–25% = 1; 26–50% = 2; 51–75% = 3, and 76–100% = 4 [35]. The Fournier intensity index was calculated for each month as the sum of all intensity categories given to each individual divided by the maximum sum that could be attributed to the community (i.e., total number of individuals multiplied by four, the highest intensity class) [12]. We also calculated the activity index, which represents the proportion of individuals or species presenting each observed phenophase for each month [12]. Previous analyses have shown that plot identity has no influence on phenodynamics of each species, thus, all calculations considered the whole study area. Although sampled individuals were previously marked [36], some of them were not identified to the species level, in which case we collected their branches when they flowered for taxonomic identification by specialists. Vouchers of these specimens were deposited in the herbaria RB and HUENF, as well as in the "PPBio inventory collection" at the Rio de Janeiro Botanical Garden (sterile samples).

2.3. Data Analysis

The activity [12] for species and individuals, and the Fournier intensity [35] and the Fournier intensity corrected by the basal area [10] for individuals were calculated monthly. The Fournier intensity corrected by the basal area (as a dominance indicator) is an adaptation of the Fournier index that considers the dimensions of the individual canopy, resulting in a more accurate estimate of quantitative phenology at the community level ([10]; see also [13]). Phenograms were constructed using activity and intensity metrics of phenophases to characterize graphically the phenodynamics of the community.

We tested the relationship between phenological events (leaf fall, leaf flushing, flowering and fruiting) and local climatic conditions using a generalized linear-mixed effects model. We used the proportion of plants at a given phenological event as a response variable, considering both activity (number of individuals in a phenological event to the total number of individuals sampled; binomial error distribution, logit link) and Fournier intensity data (activity weighted by phenological intensity; binomial error distribution, logit link; or negative binomial error distribution, see below). As a first step of data analysis, we selected four climatic variables from a total pool of nine to be used as predictors in our models. We selected the variables that were less likely to be biologically and statistically correlated, so that we could have more reliable parameter estimates in our models. These were: growing degree-days (GDD), total precipitation, number of days with rainfall (rainfall days) and photoperiod. GDD was calculated for each month as the sum of maximum and minimum temperatures, divided by two, and minus the baseline temperature. We considered the weighted mean temperature of the months of study as the base temperature, because the usual 5 °C for temperate regions is unrealistic for our study area. Photoperiod data for our study site was obtained from the National Observatory yearbook (available at http://staff.on.br/jlkm/ephemeris/index.php), and all other climate data was from the Macaé weather station.

Next, for activity and Fournier intensity data on each phenological event, we fitted a full model containing the main effects for all four predictors related to local climatic conditions, and added a random intercept term for the tree species identity and another for the year of observation nested within the tree species identity. This latter step was necessary to account for (a) differences in the phenological responses of each tree species to climatic conditions and (b) year-to-year variation in species' responses to local climatic conditions. We initially planned to include a random intercept term for the plot identity in models, but an exploratory data analysis provided weak evidence that the inclusion of such term could improve model fit to the data (Tables S2 and S3). After establishing this full model, we considered whether variation in the occurrence of phenological events was related to lagged responses to local climatic conditions. That is, whether observed phenological activity or intensity at a given month t was related to local climatic conditions in the previous month $t - 1$ (or even months before, e.g., $t - 2$ and $t - 3$). To test this idea, we fitted full models containing all climatic variables with a lag of one month, two months, three months or no lag at all in those predictors

(Tables S4 and S5). We then used Akaike Information Criterion (AIC) to compare these four models and select the appropriate lag in predictor variables to be used in all further steps of the data analyses for a given phenological event. In each case, we selected the model with the lowest AIC value, as such models are more likely to fit the data well.

We also performed two additional procedures for models using activity and intensity data for flowering, green fruits and mature fruits as response variables. First, we removed all observations from species that never exhibited these phenophases during the study period, as it made no sense to model events that never happened. In general, 80–90 species (out of the 182 species sampled) had no observations for these phenophases and were therefore excluded for the analyses as responses. Second, since there is a conditional ontogenetic dependence between an individual tree having flowering and then having fruits (green or mature; Table S6), we decided to include a lagged predictor of the previous phenophase in models for fruiting. That is, in addition to the climatic variables described above, we also included a predictor for the proportion of individuals that were flowering in the previous month ($t-1$) when we used the phenological events green fruits as a response variable. Similarly, we included a predictor on the proportion of individuals that had green fruits in the previous month when analyzing data for mature fruits. In summary, the full models took the form:

$$
\begin{aligned}
phenological\ event_t \sim \ & \beta_{GDD}x_{t-n}^{G}DD + \beta_{Total\ precipitation}x_{t-n}^{Total\ precipitation} + \\
& \beta_{Rain\ fall\ days}x_{t-n}^{Rain\ fall\ days} + \beta_{Photoperiod}x_{t-n}^{Photoperiod} + (\beta_0 + \gamma_i + \gamma_{ij}) + \varepsilon
\end{aligned}
\tag{1}
$$

where *phenological event* represents either leaf fall, leaf flush or flowering activity index (or intensity index) at a given time *t*, $\beta_{predictor\ name}$ represents the slopes for the each of the fixed predictors, *x* is the observed value of each predictor (superscripts) at the time lag $t-n$ (subscripts; n = 0, 1, 2 or 3 months). The parameters γ_i and γ_{ij} represent, respectively, the random intercept terms for differences in activity (or intensity) related to the identity of the tree species *i* and across years *j* for each tree species *i*, with β_0 being the model intercept and ε the residual error. Finally, for the phenological events related to fruiting (green and mature) the final full models were:

$$
\begin{aligned}
fruiting\ (green)_t \quad \sim \ & \beta_{GDD}x_{t-n}^{G}DD + \beta_{Total\ precipitation}x_{t-n}^{Total\ precipitation} \\
& + \beta_{Rain\ fall\ days}x_{t-n}^{Rain\ fall\ days} + \beta_{Photoperiod}x_{t-n}^{Photoperiod} \\
& + \beta_{flowering}x_{t-1}^{flowering} + (\beta_0 + \gamma_i + \gamma_{ij}) + \varepsilon
\end{aligned}
\tag{2}
$$

$$
\begin{aligned}
fruiting\ (mature)_t \quad \sim \ & \beta_{GDD}x_{t-n}^{G}DD + \beta_{Total\ precipitation}x_{t-n}^{Total\ precipitation} \\
& + \beta_{Rain\ fall\ days}x_{t-n}^{Rain\ fall\ days} + \beta_{Photoperiod}x_{t-n}^{Photoperiod} \\
& + \beta_{fruiting\ (green)}x_{t-1}^{fruiting\ (green)} + (\beta_0 + \gamma_i + \gamma_{ij}) + \varepsilon
\end{aligned}
\tag{3}
$$

Here, the fixed predictors flowering ($\beta_{flowering}$; Equation (2)) and fruiting ($\beta_{fruiting\ (green)}$; Equation (3)) were the observed activity (or intensity, when intensity data was analyzed) for those phenological events in the prior month ($t-1$).

After establishing these full models for each response variable, we used a model selection approach to determine the structure of the simplest model describing the probability of occurrence of each phenological event. Note that this probability comes from the fact that we used a generalized linear mixed-effect model using a binomial (all data based on the activity index, and leaf fall, leaf flush and mature fruits for Fournier intensity data) or negative binomial error distribution (flowering and green fruits for Fournier intensity data), which provides parameter estimates analogous to an odds ratio if they are back-transformed through exponentiation. To conduct the model selection approach, we compared the AIC values of models containing different subsets of predictors from the full model, and ranked models in ascending order according to their AIC values. Models with the lowest AIC value or with the smallest number of parameters that were within 2 AIC units from it were selected as the final best models [37]. This means that if the top-ranking model had more parameters than the

second model in the rank and their AIC difference (ΔAIC) was smaller than two units, we would favor the second model rather than the first. We standardized all predictor variables prior to the model selection, following [38] but present the estimates of the best model in their natural scale. We conducted all analysis in R-project (v.3.4.2, Stanford University, CA, USA) [39], and used the functions *glmer* and *glmer.nb* from the *lme4* package [40] for model fitting, and function *dredge* from the *MuMIn* package [41] for the model selection. We performed graphical inspections of data and residuals after establishing the models to check analyses assumptions, and used the functions available in the *DHARMa* package [42] to detect overdispersion and zero-inflation in our models – none of which was detected.

3. Results

3.1. Phenodynamics

The phenograms for activity, Fournier intensity, and intensity corrected by the basal area showed similar overall curves for leaf fall and flush in the community (Figure 2A,B,F,G). Leaf fall alternated from periods of high and low to medium activity and intensity. Leaf fall was more severe in 2007 than in 2006. The peaks and troughs of leaf fall did not match exactly with the dry- to wet-season cycle, although the events of highest leaf fall occurred in the dry seasons in all years (Figure 2A,F). In contrast, leaf flush was high in most months (above 50%), without consistent distinct periods of peaks and troughs, although a progressive reduction in leaf flush occurred from February to June in 2008 (Figure 2B,G). The values for intensity of leaf fall and flush corrected by the basal area were always smaller than 1% of the total basal area of the community (Figure 2F,G).

A total of 93 species flowered and 86 species bore fruits during the study period (Table S1). Still, both the activity and the intensity of reproductive phenophases were low over the period, especially for fruiting (Figure 2C–E,H–J). The shape of the activity and Fournier intensity curves for the reproductive phenophases were roughly similar, but they did not overlap as much as those for leaf fall and leaf flush. Differences in the flowering and fruiting phenodynamics between the two years of study also occurred, with a lower activity and intensity observed during the first year. Moreover, the values of flowering and fruiting intensity corrected by the basal area were farther away from the curves of Fournier intensity in several months (Figure 2H–J). For example, the highest flowering activity and Fournier intensity occurred from November 2008 to January 2009, while for intensity corrected by the basal area, the highest flowering was in May 2008 and in January–February 2009 (Figure 2C,H). For green fruits, the highest activity of individuals was observed between October and December 2006 and in January–February 2008, while the highest activity of species was in August 2006 and in June–July 2008 (Figure 2D). Similarly for mature fruits, the highest activity of individuals was in February 2008, and in July 2008 for species (Figure 2E). Less pronounced divergences were also observed between Fournier intensity and intensity corrected by the basal area (Figure 2I–J). Most species bore green and ripe fruits concurrently, and these two phenophases continued over long periods in many species. Finally, more than 75% of the species that set fruits were zoochoric (Table S1).
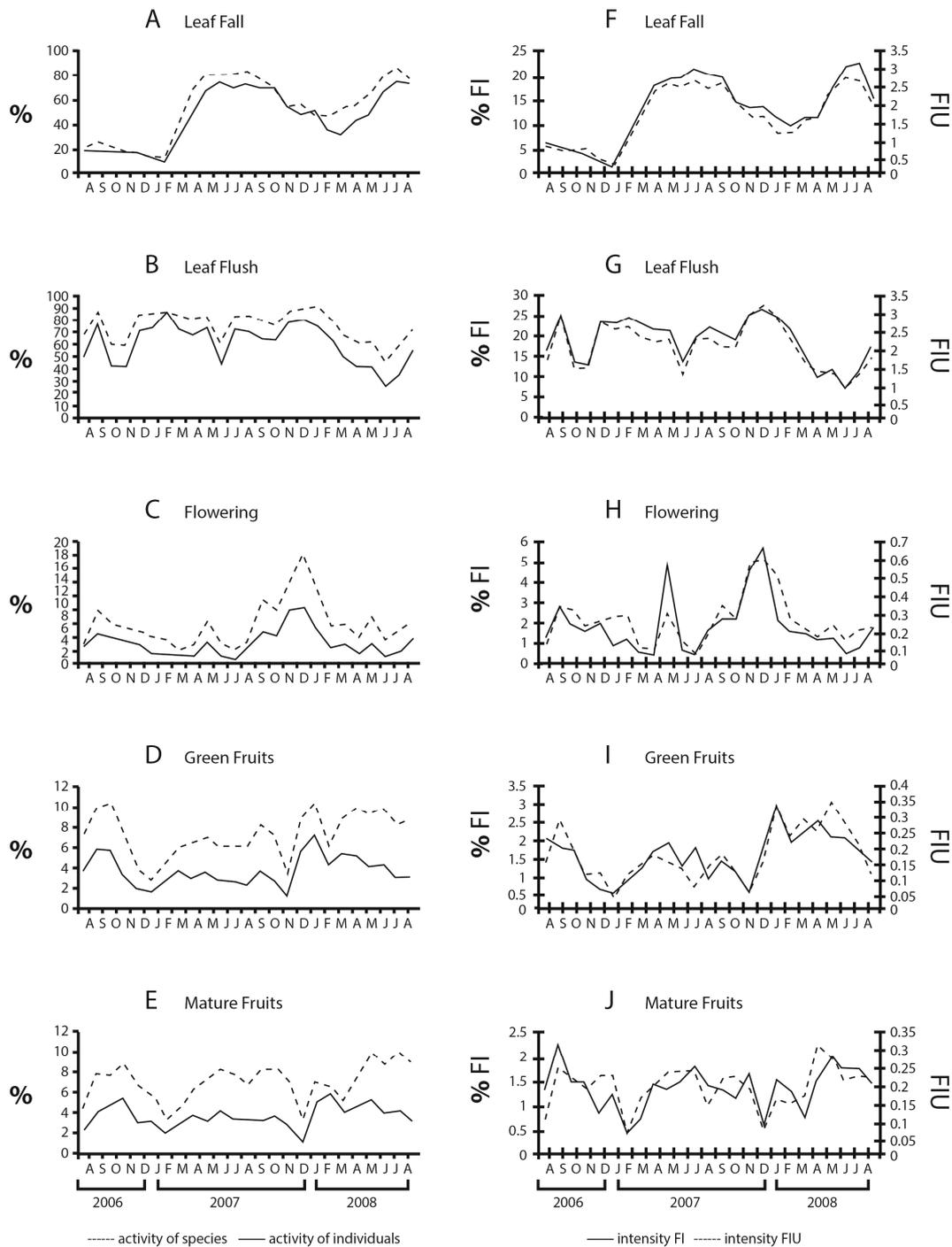
Figure 2. Vegetative and reproductive phenodynamics of tree community of lowland Atlantic Forest in the União Biological Reserve from August 2006 to August 2008 (*n* = 182 species; 479 individuals). Phenograms represent the percentage of sampled species and individuals exhibiting the phenophase each month ((**A**)–(**E**), activity data) and the percentage of Fournier intensity (FI) and the Fournier intensity corrected by the basal area (FIU) of sampled individuals each month ((**F**)–(**J**), intensity data).

3.2. The Relationship between Phenodynamics and Local Climatic Conditions

We found broadly consistent patterns between phenological activity and Fournier intensity indexes in response to local climatic conditions. As such, for simplicity, we describe the results for the phenological activity index in the main text (Tables 1 and 2) and present the results for the Fournier intensity index in the Supplementary Material (Tables S7 and S8). In addition, the results we report do not differ whether inferences are drawn based on the top ranking model or by model averaging the fixed predictors in the confidence set for each response variable (Tables S9 and S10).

Table 1. Models that were better supported by the data according to the Akaike Information Criteria (AIC) for data on phenological activity on (a) leaf flush, (b) leaf fall, (c) flowering, (d) fruiting (green), and (e) fruiting (mature). We fitted a mixed-effects model using a binomial distribution (link logit) for each response variable and conducted a model selection, whereby we ranked models according to their AIC values, and selected the models within ΔAIC $\leq$ 2 of the model with the lowest AIC value for inference. The Akaike weight for a given model, w_i, represents the probability that a given model is the best model in the set, and the ratio of w_i between models can indicate the strength of evidence in favor of one model over the other. The column 'Lag' refers to the selected lag used for the predictor variables photoperiod, growing degree-days, total precipitation, and rainfall days in the models. When "Flowering" and "Fruiting (green)" appear as predictors in a given model, they represent whether a given individual was in that phenophase in the previous month. * denotes the final model for data on each phenophase, which was selected based on the smallest number of predictors within ΔAIC $\leq$ 2. Df: represents the degrees of freedom.

Model	Lag	Df	logLik	AIC	ΔAIC	w_i
(a) Leaf flush						
~Photoperiod + Growing degree-days + Rainfall days	Lag 0	6	−4372.27	8756.54	0.00	0.46
~Growing degree-days + Rainfall days + Total precipitation	Lag 0	6	−4373.16	8758.31	1.77	0.19
~Photoperiod + Growing degree-days + Rainfall days + Total precipitation	Lag 0	7	−4372.21	8758.42	1.88	0.18
~Growing degree-days + Rainfall days *	Lag 0	5	−4374.27	8758.53	1.99	0.17
(b) Leaf fall						
~Photoperiod + Growing degree-days + Total precipitation	Lag 0	6	−4125.22	8262.43	0.00	0.49
~Photoperiod + Total precipitation *	Lag 0	5	−4126.66	8263.32	0.88	0.32
~Photoperiod + Growing degree-days + Rainfall days + Total precipitation	Lag 0	7	−4125.19	8264.37	1.94	0.19
(c) Flowering						
~Photoperiod + Growing degree-days + Total precipitation *	Lag 0	6	−931.91	1875.81	0.00	0.62
(d) Fruiting (green)						
~Flowering + Rainfall days *	Lag 2	5	−855.58	1721.17	0.00	0.43
~Flowering + Rainfall days + Total precipitation	Lag 2	6	−855.23	1722.46	1.30	0.23
~Growing degree-days + Flowering + Rainfall days	Lag 2	6	−855.47	1722.94	1.78	0.18
~Photoperiod + Flowering + Rainfall days	Lag 2	6	−855.56	1723.12	1.96	0.16
(e) Fruiting (mature)						
~Fruiting (green) *	Lag 1	4	−613.47	1234.95	0.00	0.24
~Fruiting (green) + Rainfall days	Lag 1	5	−612.59	1235.17	0.23	0.21
~Fruiting (green) + Rainfall days + Total precipitation	Lag 1	6	−612.09	1236.17	1.23	0.13
~Growing degree-days + Fruiting (green)	Lag 1	5	−613.18	1236.35	1.41	0.12
~Growing degree-days + Fruiting (green) + Rainfall days	Lag 1	6	−612.28	1236.57	1.62	0.11
~Photoperiod + Fruiting (green)	Lag 1	5	−613.36	1236.71	1.76	0.10
~Fruiting (green) + Total precipitation	Lag 1	5	−613.47	1236.94	2.00	0.09

Table 2. Slopes, standard errors (SE), *z* and *p* values, and the lag used for each predictor included in the final models for data on phenological activity on (a) leaf flush, (b) leaf fall, (c) flowering, (d) fruiting (green), and (e) fruiting (mature). In each case, we used the structure of the model with the smallest number of predictors within ΔAIC $\leq$ 2 units of the model with the lowest AIC for each response variable, as shown in Table 1. When "Flowering" and "Fruiting (green)" appear as predictors in a given model, they represent whether a given individual was in that phenophase in the previous month.

Predictor	Lag	Slope	SE	*z*	*p*
(a) Leaf flush					
Intercept		−0.52	0.02	−30.34	<0.001
Rainfall days	lag 0	−0.22	0.03	−7.02	<0.001
Growing degree-days	lag 0	0.32	0.03	10.31	<0.001
(b) Leaf fall					
Intercept		−0.91	0.04	−25.87	<0.001
Total precipitation	lag 0	−0.38	0.05	−8	<0.001
Photoperiod	lag 0	−0.55	0.04	−13.24	<0.001
(c) Flowering					
Intercept		−3.34	0.1	−33.84	<0.001
Total precipitation	lag 0	−0.64	0.14	−4.44	<0.001
Photoperiod	lag 0	1.4	0.17	8.29	<0.001
Growing degree-days	lag 0	−0.61	0.16	−3.8	<0.001
(d) Fruiting (green)					
Intercept		−3.27	0.14	−22.56	<0.001
Flowering	lag 1	1.48	0.27	5.52	<0.001
Rainfall days	lag 2	−0.24	0.11	−2.29	0.022
(e) Fruiting (mature)					
Intercept		−5.85	0.27	−22.05	<0.001
Fruiting (green)	lag 1	5.72	0.33	17.54	<0.001

Leaf flush, leaf fall and flowering were all related to local climatic conditions at the time of sampling (no lagged responses), while fruiting (green and mature) was often related to local climatic conditions from months prior to observations (lags = 1 or 2; Table 1; Tables S7 and S8). In general, the probability of occurrence of phenological events responded differently to local climatic conditions depending on the phenophase. For example, the probability of leaf flush decreased with the number of rainfall days across tree species (estimate = −0.22, *p* < 0.001; estimated is not back-transformed), but increased with growing degree-days (estimate = 0.32, *p* < 0.001; see Table 2 for estimates of the final model of each phenophase). Leaf fall, on the other hand, decreased both with the photoperiod and total precipitation. Similarly, while flowering activity decreased with total precipitation and growing degree-days, it increased with photoperiod. Finally, the probability of occurrence of green fruits decreased with the number of rainfall days, and no climatic variable explained the probability of occurrence of mature fruits (for example, *p* = 0.073 for growing degree-days in the final model). The proportion of individuals flowering in the previous month was a strong predictor of the probability of occurrence of green fruits, while the proportion of individuals with green fruits predicted the probability of occurrence of mature fruits (Table 2). An exploratory analysis on species-specific deviation from these overall patterns revealed that we were able to describe the variation in phenophases in relation to local climatic conditions reasonably well for most of the species (Figures S3–S7).

4. Discussion

The phenodynamics of lowland rainforests has been studied for decades, but their relationships with the phytosociological structure of the community and the synergistic action of local climatic conditions are still poorly understood. Here, we present the community phenodynamics from a

lowland Atlantic Forest, considering the basal area of tree species in the sampling area. Our results confirm that Rebio União harbors evergreen forest, although leaf fall was more intense in the dry season. We also recorded a low expression of the reproductive phenophases, which reflects the failure of many individuals to flower every year and the likely constraints on the trees for fruit production and maturation. Lastly, we found that the probability of occurrence of phenological events was related to local climatic conditions, especially to differences in photoperiod, rainfall distribution, and long-term temperature trends over the year—with some consistency across tree species. In the following sections we discuss our main findings, taking into consideration the current knowledge of the phenological patterns of Neotropical forest communities.

4.1. Vegetative Phenophases

Information on vegetative phenological dynamics is essential for accurate vegetation classification [43,44]. Leaf fall and leaf flush events occurred simultaneously at Rebio União, as typically found in lowland tropical forests [26,45], although total precipitation in Rebio União is lower than thresholds commonly associated to rainforests. In spite of the high activity and moderate Fournier intensity of the vegetative phenophases, their amplitude in terms of the intensity corrected by basal area was low. This result reflects the continued, low-intensity occurrence of both leaf fall and leaf flush with respect to canopy cover, and hence supports the characterization of the community as evergreen (after [19,46]). Concerning forest classifications, the system of Frankie et al. [19] is based only on the percentage of species that fit into a certain category (i.e., evergreen, semideciduous, and deciduous) regardless of differences among species in the time of leaf phenological events (leaf fall and leaf flush). The system proposed by Oliveira-Filho [46] goes one step further, as it uses the same three categories but establishes that in evergreen forests less than 30% of the leaf mass is lost in the dry season. Therefore, classifying vegetation in these categories requires information on the intensity of phenodynamics, which improves the classification if combined with data on structural parameters, such as the metrics that weight the intensity of phenophases by the basal area (e.g., [10]).

Precipitation, temperature, and photoperiod were related to vegetative phenophases at Rebio União. Several studies have indicated that small changes in temperature influence vegetative phenophases of trees across tropical forests [19,24,26,47]. Conversely, until the 2000s, few studies in the Neotropics indicated that photoperiod is an important factor in regulating phenology (e.g., [25]); although, in his seminal study, Alvim [48] suggested that photoperiod and vegetative phenophases in tropical forests are related. In fact, evidence for the role of photoperiod in foliar dynamics of tropical communities has accrued. Predictor variables of leaf fall dynamics in our study (i.e., photoperiod and total precipitation) were consistent with expectations for moderate- and fast-acting ecophysiological responses. Specifically, photoperiod is a reliable signal for temporal cycles, even in regions with low seasonality [22,23,26,49]. Also, in tropical forests from higher latitudes, annual variation in photoperiod anticipates movements of the intertropical convergence zone and seasonal changes in precipitation, irradiance and biotic activity [50]. On the other hand, periods of reduced precipitation amounts affect soil water availability, and such temporal soil droughts may hasten the abscission of senescent leaves with reduced control of transpiration, so the leaf fall dynamics tracks rainfall regime at Rebio União (i.e., proximate cues) [50,51].

Another factor related to the vegetative phenodynamics at our study site was rainfall distribution. Here we found a negative relationship between the number of days with rainfall and leaf flush activity and intensity, indicating that the monthly distribution of precipitation influences this phenophase. However, the mechanism underlying this relationship is not clear. An experimental study providing irrigation during the dry season in a lowland tropical rainforest found that changes in the amount of available water did not alter the behavior of the vegetative phenophases of evergreen species [51]. However, a study conducted in the Amazon showed that leaf production remains constant or increases in the dry season [52]. Accordingly, it was suggested that rainfall distribution may influence phenological behavior indirectly, because the greater cloud cover on rainy days reduces the amount of

solar irradiance that plants receive, resulting in lower photosynthetic activity and a reduced production of new leaves [25,53].

Based on our results and considering the scenarios of increasing average global temperatures within the range of 0.3 to 4.8 °C by 2100 [54], we could expect an intensification of leaf phenological cycles and, consequently, in carbon uptake in the forests at Rebio União. However, projections from climate models for tropical regions indicate a higher number of rainless days by 2100, in which temperatures will likely exceed the upper limit of the thermal range required for plant growth [55]. Thus, the association we found between the number of days with precipitation and leaf fall dynamics agrees with the view that the greater potential for extreme events (e.g., heat waves or drought) may impair plant growth and even cause tree mortality in tropical forests [56].

4.2. Reproductive Phenophases

The time and amplitude of the reproductive phenophases were irregular during the two years of observations. For instance, the highest flowering activity and Fournier intensity occurred, as expected, during the 2008–2009 wet season; however, the same did not occur in the previous wet season. Long-term studies have indicated that abnormal climate events are the main cause of different flowering patterns in certain years, for instance associated with the El Niño-Southern Oscillation dynamics [57–60]. In general, it is not possible to identify the probable reasons for phenological differences between years in short-term studies, unless a clear influencing factor has occurred atypically in the period of study [61]. The only climatic condition that differed markedly from the climate normal in the 2006 dry season was temperature, due to its larger variation between minimum and maximum values in May, June, and July of that year (Figure 1). Accordingly, GDD was negatively related with flowering activity in the Rebio União. Flowering and fruiting differences over the years of study, together with wide oscillation in the flowering curves (i.e., sequences of months alternating peaks and troughs) indicate that anthophilous and frugivorous animals likely faced marked fluctuations in resource availability during the years of study. These temporal fluctuations are not limited to the seasonal patterns of higher and lower availability, a well-known phenomenon even for tropical forests in areas with low climate seasonality (e.g., [62,63]). Our results showed that wide variations in the resource levels may occur between subsequent months and seasons across years. Such variations may correspond to records according interruption of the sequential resource availability in tropical forests [30].

Several studies suggest that photoperiod is the main element driving flowering activity of tropical tree species [23,64,65] but there are obvious caveats to this conclusion. For instance, Stevenson et al. [27] argued that given that photoperiod is independent of the local weather, if flowering was mainly regulated by it, species should flower in similar periods every year, regardless of the fluctuation in climatic conditions. In fact, flowering activity consistently responded to photoperiod variation for only 23% of the species in their study in a lowland rainforest in Colombia [27]. Accordingly, we have found that flowering dynamics were related to photoperiod (positively), and total precipitation and GDD (negatively). Similarly, flowering responses to rainfall and temperature were also found in other lowland Atlantic Forest tree communities in southeastern Brazil [60], in which more intense flowering events were observed after periods of lower precipitation and mean temperature.

We found a predominance of zoochory and scattered fruiting that oscillates within a narrow range of low activity and intensity. This phenodynamic seems to predominate in tropical rainforests, which could reflect the prevalence of lengthy fruit development, added to the many species that display mature fruits gradually in these forests [11,26,62]. Only precipitation in the previous month was related to the phenological activity of green fruits in our study site. However, flowering and green fruit of the months prior to the observation of the event were more strongly associated to green and mature fruits' dynamics, respectively. In this sense, we suggest that fruiting dynamics tracks the occurrence of biologically related phenophases, and associations between fruiting phenodynamics and climatic conditions seem to be only indirect, affecting fruit development and production (see [66]).

The phenodynamics curve of flowering intensity corrected by the basal area differed from the curves of the other dependent variables. The most remarkable difference was the peak of corrected intensity in the 2007 dry season, when few species were flowering, which resulted from an intensive flowering of some species that dominate in the community. Similar discrepancies were recorded for fruiting dynamics. These results illustrate the limitation of the most usual methods of data collection in field studies and phenological analyses for assessing community phenodynamics with respect to canopy cover [10]. Therefore, disregarding structural parameters in the phenological characterization of forest communities may be misleading. The most evident biases are related to estimates of resource availability for nectarivores and frugivores at the community level, which are crucial to a better understanding of patterns, processes and mechanisms involving mutualistic plant-animal interactions in tropical forests (e.g., [13]). More accurate estimates of the reproductive phenodynamics for those communities are also essential to assess their impacts on ecosystem functioning, due to the expected increase in the frequency and intensity of climate extremes during the 21st century (reviewed by [30]).

Episodes of high fruit production associated to El Niño events followed by low fruit production in years that follow occur widely across Neotropical forests, but there is no equivalent of the mass-fruit events at multiyear intervals seen in Asian forests [59]. Thus, a regular fruit supply with famines at multiyear intervals is the general pattern in Neotropical forests [59]. However, the low degree of flowering and fruiting activity and intensity seems to be a pattern for Atlantic Forest tree communities [29,60,67] that in combination with fragmentation may compromise forest dynamics, since forest edges have low densities of seedlings [36]. Floral and fruit resources for the fauna are obviously not restricted to the tree assemblage, and a more comprehensive view will depend on phenological studies encompassing epiphytes, vines, lianas, and understory herbs, shrubs and treelets. A few phenological studies at the community level were conducted for other life-forms than trees in the Atlantic Forest (e.g., [45,68]), in particular for lowland rainforests. These other plant groups certainly provide additional resources for pollinators and frugivores, but in any case, the repeated records of a low degree of flowering and fruiting for trees, observed in different studies in the Atlantic Forest, highlight concerns regarding the effects of global climate change in this biodiversity hotspot.

5. Conclusions

Here we show that precipitation, temperature and photoperiod are linked to the phenodynamics across tree species in a lowland Atlantic Forest. We applied an analytical approach to delimit the contribution of each of the climatic conditions to the occurrence of phenological events, which can be considered a first step toward unveiling the mechanisms underlying phenological patterns in high-diversity tropical communities. With a few exceptions [13], phenological studies on tropical rainforest communities have not incorporated the structural parameters of vegetation, such as species abundance or canopy coverage. Although useful in many aspects, phenograms and correlations of these species-based studies are biased representations of the dynamics of the intensity of phenophases in the community [10]. Here we found important differences in community phenodynamics, in particular for flowering and fruiting, after integrating the species' basal area into phenological curves. Moreover, we generated a more cohesive evaluation of the association between the community phenology and climate, taking into account multiple effects of local climatic conditions as well as the influence of ontogenetically related phases in the fruiting phenodynamics. Thus, our study indicates some improvements that can be made to the statistical modelling of vegetation dynamics in response to local climatic conditions for tropical rainforests (see also [27]).

Over larger scales, ground-based phenology is also important to validate and calibrate global vegetation models used to predict the effects of future climate change on ecosystems [69,70]. Consistent data that permits the determination of the intensity of phenophases per area per month are scarce for tropical rainforests. This kind of information, as provided in our study, may be useful for more accurate calibration of models of global vegetation dynamics at the regional scale, and better estimates when applied on wider scales. Finally, several ecophysiological studies have indicated that the

regulation of phenological events of tropical trees is species-specific [71]. Accordingly, our results may in part represent spurious associations with non-causal variables, in spite of the fit of the data to our models. Therefore, additional systematic measurements of phenology and ecophysiological mechanisms are necessary to improve the predictability of the effects of global climate change on tropical forest dynamics.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/9/3/114/s1, Table S1: List of the species studied in the Rebio União and their respective identification codes (ID code), family, number of observed individuals (No. ind.), basal area (DBA), dispersal syndrome (ane = anemochory; zoo = zoochory), and flowering and fruiting times, from August 2006 to August 2008., Table S2: Comparison of models with different fixed effects (models without or with lagged predictors) and random effects terms (with or without plot identity random effect term) by means of their AIC values for activity data on (a) leaf flush, (b) leaf fall, (c) flowering, (d) fruiting (green), and (e) fruiting (mature), Table S3: Comparison of models with different fixed effects (models without or with lagged predictors) and random effects terms (with or without plot identity random effect term) by means of their AIC values for intensity data on (a) leaf flush, (b) leaf fall, (c) flowering, (d) fruiting (green), and (e) fruiting (mature). Table S4: Comparison among models containing predictors with different lags when analyzing data on phenological activity for (a) leaf flush, (b) leaf fall, (c) flowering, (d) fruiting (green), and (e) fruiting (mature). Table S5: Comparison among models containing predictors with different lags when analyzing data on phenological intensity for (a) leaf flush, (b) leaf fall, (c) flowering, (d) fruiting (green), and (e) fruiting (mature). Table S6: Pearson correlation coefficients between each of the five phenophases for (a) activity and (b) intensity data, Table S7: Models that were better supported by the data according to the Akaike Information Criteria (AIC) for data on phenological intensity on (a) leaf flush, (b) leaf fall, (c) flowering, (d) fruiting (green), and (e) fruiting (mature). Table S8: Intercept (β0), Slopes, standard errors, z and p values, the lag used for each predictor included in the final models for data on phenological intensity on (a) leaf flush, (b) leaf fall, (c) flowering, (d) fruiting (green), and (e) fruiting (mature). Table S9: Standardized effect size estimates, standard errors, 95% confidence intervals, and z and p values for each predictor included in the averaged model for activity data on (a) leaf flush, (b) leaf fall, (c) flowering, (d) fruiting (green), and (e) fruiting (mature). Table S10: Standardized effect size estimates, standard errors, 95% confidence intervals, and z and p values for each predictor included in the averaged model for intensity data on (a) leaf flush, (b) leaf fall, (c) flowering, (d) fruiting (green), and (e) fruiting (mature). Figure S1: Location of the União Biological Reserve in the State of Rio de Janeiro, Brazil, and satellite image of the reserve during the study, showing the sampling plots. Figure S2: Satellite image of the União Biological Reserve after the enlargement of its area on June 5, 2017. Source: Google Earth 2017. Figure S3. Species-specific deviation from the intercept for the model on the variation in the probability of leaf flushing using phenological activity data. Figure S4: Species-specific deviation from the intercept for the model on the variation in the probability of leaf fall using phenological activity data. Figure S5: Species-specific deviation from the intercept for the model on the variation in the probability of flowering using phenological activity data. Figure S6: Species-specific deviation from the intercept for the model on the variation in the probability of fruiting (green) using phenological activity data. Figure S7: Species-specific deviation from the intercept for the model on the variation in the probability of fruiting (mature) using phenological activity data.

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