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Original Article

What triggers phenological events in plants under seasonal environments? A study with phylogenetically related plant species in sympatry

O que desencadeia eventos fenológicos em plantas em ambientes sazonais? Um estudo com espécies de plantas filogeneticamente relacionadas e em simpatria

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Abstract

In this study, we evaluated variation in vegetative and reproductive phenological events of four phylogenetically related plant species subjected to a seasonal environment. To this aim, we sampled 15 individuals of each plant species every fortnight for one year, between January and December of 2017. To assess when a given phenophase occurred more intensely in the population, the Fournier intensity index was used and the synchrony of individuals of the sample in a given phenological event was estimated using the activity index. The Rayleigh (Z) test was used to determine whether the phenological events have seasonal distribution. The relationship of abiotic factors (photoperiod, precipitation, relative humidity and temperature) with the intensity of phenophases was evaluated for each plant species using generalized linear models (GLMs). The phenophases of all plants showed a seasonal distribution pattern, as well as variation in synchrony of phenophases and specific sets of abiotic factors significantly influenced their phenophases. New leaves, for example, were produced throughout the seasons, with intense leaf fall in the dry season. Flowering periods, on the other hand, did not overlap. Indeed, species exhibited sequential flowering and asynchronous flowering among individuals. Our results suggest that the phenological patterns of four sympatric plant species are directly linked to climatic variables, but different abiotic factors affected different phenophases.

Keywords: Cerrado, Malpighiaceae, phenology, phenophases, sequential flowering.

Resumo

Neste estudo, avaliamos a variação nos eventos fenológicos vegetativos e reprodutivos de quatro espécies de plantas filogeneticamente relacionadas submetidas a um ambiente sazonal. Para isso, amostramos 15 indivíduos de cada espécie quinzenalmente, pelo período de um ano, entre janeiro e dezembro de 2017. Para avaliar quando uma determinada fenofase ocorreu de modo mais intenso na população foi utilizado o índice de intensidade de Fournier e a sincronia dos indivíduos da amostra em determinado evento fenológico foi estimada utilizando-se o índice de atividade. O teste de Rayleigh (Z) foi usado para determinar se os eventos fenológicos têm distribuição sazonal. A relação dos fatores abióticos (fotoperíodo, precipitação, temperatura e umidade relativa) com a intensidade das fenofases foi avaliada para cada espécie de planta usando modelos lineares generalizados (GLMs). As fenofases de todas as plantas apresentaram um padrão de distribuição sazonal, bem como variação na sincronia das fenofases e conjuntos específicos de fatores abióticos influenciaram significativamente suas fenofases. Folhas novas, por exemplo, foram produzidas ao longo das estações, com intensa queda de folhas na estação seca. Os períodos de floração, por outro lado, não se sobrepuseram. De fato, as espécies exibiram floração sequencial e floração assíncrona entre os indivíduos. Nossos resultados sugerem que os padrões fenológicos das quatro espécies de plantas simpátricas estão diretamente ligados às variáveis climáticas, mas diferentes fatores abióticos afetaram diferentes fenofases.

Palavras-chave: Cerrado, Malpighiaceae, fenologia, fenofases, floração sequencial.

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1. Introduction

Plant phenophases are intimately related to climate (Lieth, 2013) and temperature is one of the main drivers of plant phenology in vegetations worldwide (e.g., tropical forests: Lima et al., 2021; savannas: Vilela et al., 2017). Phenological studies are, therefore, crucial to understand how plant growth and reproduction vary according to climate, especially during the Anthropocene, as shifting phenological events (e.g., early reproduction, late leaf flushing) due to changes in temperature and precipitation regimes might affect plant community structure, associated animals such as herbivores and pollinators (Vilela et al., 2017) and ultimately the provision of ecosystem services (Memmott et al., 2007).

Plants, like other organisms, have developed adaptations to express their phenophases at optimum scenarios of climate. In tropical savannas, for instance, leaf fall is generally concentrated in the dry season (Williams et al., 1997; Novaes et al., 2020) and leaf flushing, which is less seasonal, can occur in both the dry and wet seasons (Lacerda et al., 2018). Phenological adaptations in these harsh environments include flowering in the dry season, when plants become more visible to mutualistic animals due to leaf fall (Williams et al., 1997), or flowering at the very beginning of the rainy season (just before the heavier rains) a strategy to avoid flower damage (Novaes et al., 2020). Furthermore, plants usually flower asynchronously in populations or communities, a common strategy to avoid competition for visitors and pollinators, promoting pollinator assurance and maximizing intraspecific pollen transfer (Janzen, 1980; Mendes et al., 2011). Zoochoric fruits are usually produced along the year, allowing for a greater supply of resources for frugivores, whereas anemochoric or autochoric fruits are produced during the dry season, when conditions are more favorable to diasporte dispersion (Kuhlmann and Ribeiro, 2016).

Climatic variables are subject to yearly fluctuations and have been suggested as important drivers of vegetative and reproductive cycles of plant species in seasonal environments (Borchert, 1999; Novaes et al., 2020). Short-day plants are induced to flower in the dry season with the shortening of the photoperiod, and long-day plants usually flower in the rainy season, influenced by extended photoperiods (Schwabe and Wimble, 1976). Precipitation is another common abiotic driver of the growth of Cerrado plants (Vilela et al., 2017), usually favouring plant vegetative growth. On the other hand, droughts can reduce plant growth and lead to leaf fall, as well as changes in flower and fruit production, ceasing plant cycle when prolonged (Opler et al., 1976; Borchert, 1999). Temperature has also been associated with the triggering of reproductive phenophases, which may promote or block the production of metabolites from some genes, whose action is directly linked to vegetative growth or flowering control (Singh et al., 2017).

Plant development and reproduction are closely linked to both biotic and abiotic factors (Novaes et al., 2020) and the study of the phenology of tropical plants becomes increasingly essential not only for the conservation of plant diversity, the maintenance of asociated fauna and associated ecosystem services, but also to understand the impacts of climate change. Seasonal tropical environments are being impacted by global warming (e.g., increased temperatures and changes in the amount of rainfall) (Mendoza et al., 2017) which can directly affect the reproductive success of plants (Vilela et al., 2017) and indirectly affect the dynamics of communities (Memmott et al., 2007).

In this study, we assessed how climatic variables might trigger the phenological phases of four sympatric and related plant species in a seasonal environment, investigating four plant species of the Malpighiaceae family, which have very similar floral resources - *Banisteriopsis campestris* (A.Juss.) Little, *Byrsonima verbascifolia* (L.) DC., *Heteropterys umbellata* A.Juss. and *Peixotoa tomentosa* A.Juss. We tested the following hypotheses: (i) the phenophases of these plant species present seasonal rhythms; (ii) these plant species do not overlap their floral resources; and (iii) the phenophases of these plant species are influenced by different climatic variables. In light of these hypotheses, we made the following predictions: (i) Plant species produce leaves during the transition from the wet to the dry season, with leaf fall mainly at the end of the dry season, and reproductive phenophases occur during the wet season; (ii) These plant species present floral asynchrony; and (iii) The vegetative phenophases are more conditioned by rainfall, and the reproductive phenophases are mainly explained by the temperature. To test the above-mentioned hypotheses, we investigated the vegetative and reproductive phenophases of these plant species for one year and evaluated how different climatic variables influenced the triggering of these phenophases.

2. Material and Methods

2.1. Study site

The study was conducted in the Área de Proteção Ambiental (APA) São José, in Minas Gerais, southeastern Brazil. The mountain has 4,758 hectares and is located between the coordinates of 21°03-07'S and 44°06-13'W. It has a very rugged relief, with outcrops of quartzitic sandstone striking in the landscape, with altitude ranging from 800 to 1400 m (Henriques et al., 2019). The climate is subtropical in altitude (Cwb) according to the Köppen classification (Alvares et al., 2014), with dry winters and mild summers, with an average annual rainfall of 1,435 mm and an average annual temperature around 19 °C (Pereira et al., 2020). The vegetation is diverse, presenting several ecotypes within a radius of just 1 km. The seasonal semideciduous forest is the dominant vegetation to the South and Cerrado phytophysiognomies occur in the North and East, with the formation of cerrado *sensu stricto*. In the higher elevations vegetation of campo rupestre predominates (Pereira et al., 2020). Data were collected in an area of 3 ha composed of cerrado *sensu stricto* in the western portion of the mountain, in the municipality of Tiradentes (21°06'23"S and 44°12'11"W).

2.2. Study system

We evaluated a system composed of four plant species within the Malpighiaceae family that coexist in the cerrado *sensu stricto* of the study area, ranging from sub-shrubs to small trees. These plant species have similar flowers with 5 petals, bilaterally symmetrical and with elaiophores at the base of the sepals. They produce nectar, pollen, and oil as floral resources (Figure 1).

B. campestris is a sub-shrubby species, usually measuring 20 to 60 cm in height. The leaves are light green, membranous, with a well-marked vein, with hair on both sides, and having a pair of extrafloral nectaries at the base of the main vein. The flowers are unguiculated and fringed pink, the standard petal being higher than the others. The calyx has five sepals with eight elaiophores. The fruits are dry samara type, anemochoric, with one to four dispersion units per fruit (Souto and Oliveira, 2008).

B. verbascifolia is a shrub-tree species, has a stem of up to 37 cm in diameter, and can reach 4 m in height. The leaves are leathery, discolored, hairy, and grayish on the abaxial face. It has axillary stipules. The inflorescences have terminal racemes pendant. The petals are yellow, unguiculated, fringed, with four of them curved and a smaller one erect. The petals are orange after pollination. The calyx has five sepals with a pair of elaiophores in each sepal. The fruits are drupes up to 2.5 cm in diameter, zoochoric, globoid, yellowish, and with a persistent calyx (Mamede, 1987).

H. umbellata is an erect, sub-shrubby species, usually 40 to 80 cm tall. It has membranous leaves, a limb with two extrafloral nectaries at the base. The flowers are yellow and have eight elaiophores at the base of four sepals, distributed in pairs. The petals are unguiculated and fimbriated. The standard petal flowers produce up to four-winged samara seeds with 1.5 cm long, ascending, and with a seminiferous nucleus (Mamede, 1987).

P. tomentosa is a sub-shrubby species, with one or two branches that can reach 3 m in height. It has few leaves, which are tomentosa on both sides. It has a pair of extrafloral nectaries at the base of the leaf blade on the abaxial face (Del-Claro, 1998). Its flowers are yellow and have eight elaiophores at the base of four sepals, distributed in pairs. The petals are unguiculated and fimbriated. The standard petal is higher. The flowers produce up to four-winged samara seeds (Mamede, 1987).

2.3. Data sampling

For the analysis of phenological events, 15 individuals of each plant species were marked, totaling 60 plants. Marked plants were at least 10 meters apart and submitted to similar environmental conditions in an area of 2.50 ha composed exclusively of cerrado *sensu stricto* under the same type of

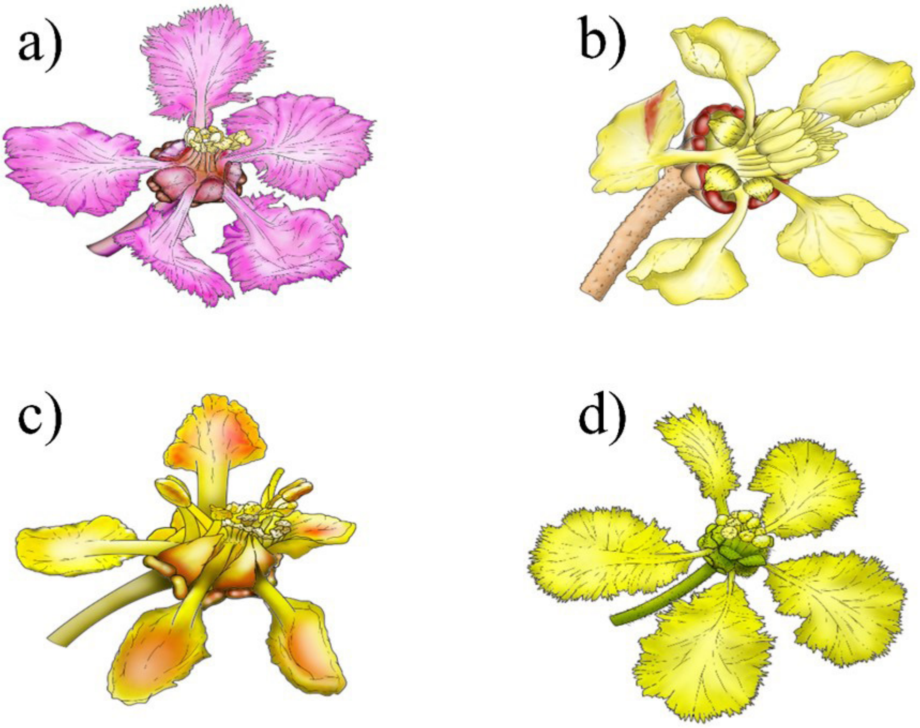

Figure 1. Illustration of the flowers of the four plant species of the Malpighiaceae family studied in the cerrado *sensu stricto* of the Serra de São José Environmental Protection Area, Tiradentes, MG, Brazil. (a) *Banisteriopsis campestris*, (b) *Byrsonima verbascifolia*, (c) *Heteropterys umbellata*, and (d) *Peixotoa tomentosa*. All flowers measure approximately 3cm in diameter, having five unguiculated petals, five sepals with elaiophores at the base, and provide nectar, pollen, and oil as floral resources.

soil (yellow latosol) and similar altitude (approximately 1040 m). The plants were monitored fortnightly for one year, between January and December 2017. The following vegetative phenophases were observed: leaf flushing, mature leaves, and leaf falling; and the reproductive stages: flower buds, flowering, and fruiting.

To assess when a given phenophase occurred more intensely in the population, the Fournier Intensity Index was used, through a scale of five intensity categories (0 to 4), where 0 indicates the absence of phenophase in the individual; 1: 1 to 25%; 2: 26 to 50%; 3: 51 to 75%; and 4: 76 to 100% of the phenophase. The intensity of the phenophases was calculated by the equation: [% Fournier = (∑ Fournier / 4 N) × 100], where ∑ Fournier = sum of categories for each individual and N = number of individuals present in the population sample (Fournier, 1974).

We also evaluated the synchrony of individuals in the sample in a given phenological event. We used the Activity Index proposed by Bencke and Morellato (2002), in which asynchronous phenological events present less than 20% of individuals in phenophase, slightly synchronous from 20% to 60% of individuals in phenophase and high synchrony those with more than 60% of individuals in phenophase.

Abiotic data were collected for the period of study at INMET (Instituto Nacional de Meteorologia), in the database of the automatic station of São João del-Rei, located 5 km from the study area (INMET, 2018).

2.4. Data analysis

To describe the phenological behavior and examine the occurrence of seasonal patterns, we performed circular statistical analyses. For this, the 24 fortnights of the study period were converted into angles to obtain the angle of the mean vector (μ), the median, the standard error of mean, the length of mean vector (r), which varies from 0 when there is phenophase frequency dispersion and mean angle cannot be described, for 1, when all data are concentrated in the same direction (Morellato et al., 2010), and the Rayleigh test (Z) of circular uniformity for each phenophase of all plant species (Zar, 2010). All analyses were conducted on Oriana software (Kovach, 2011).

To investigate which climatic variables best explained the triggering of vegetative and reproductive phenophases of plant species, we performed generalized linear models (GLMs). For this, we examined the relationship between the mean values of photoperiod, relative humidity and temperature, and the accumulated values of precipitation of the 24 fortnights of the study (Table S1, Supplementary Material 1) with the values of intensity of the phenophases of the plant species. All analyses were conducted using lme4 package (Bates et al., 2011) in R software (R Core Team, 2021).

3. Results

3.1. Intensity index

The phenophases of the species showed a seasonal distribution pattern ($P < 0.0001$), except for the leaf flushing of *P. tomentosa*, which had a uniform distribution ($Z = 0.647$, $P = 0.524$) and phenophase frequency dispersion (length of mean vector (r) = 0.031) (Figures 2 to 5 and Table 1).

The four plant species studied showed similar phenological patterns for vegetative phenophases. The plants produced new leaves over the two seasons, with intense leaf reduction in the dry season (Figures 2 to 5 and Table 1). However, the flowering peaks of these species did not overlap, presenting a sequential flowering pattern (mean vector (μ): *B. verbascifolia*, 269.503° = September/2; *H. umbellata*, 301.224° = November/1; *P. tomentosa*, 1.559° = January/1; and *B. campestris*, 40.403° = February/1) (Figures 2 to 5 and Table 1). Regarding fruit production, *B. campestris* and *H. umbellata* fruited only in the rainy season, with their intensity frequencies concentrated in the same direction (length of mean vector (r) > 0.9), while *B. verbascifolia* and *P. tomentosa* produced fruits at low intensity over the two seasons, with the length of mean vector (r) < 0.4 (Figures 2 to 5 and Table 1).

3.2. Activity index

The four plant species studied varied throughout the year concerning the synchrony of their individuals, especially in their reproductive phenophases. Thus, their individuals had high synchrony for leaf production and leaf falling, but the production of flowers and fruits varied from asynchronous to highly synchronous (see information about each plant species in the Suplementary Material S2, Figures S1 to S4).

3.3. The influence of climatic variables on phenophases

The relative humidity was the most determining factor to explain the variation in the phenophases of the studied species (12 phenophases in total), followed by temperature (11 phenophases), photoperiod (9 phenophases), and precipitation (4 phenophases). Vegetative phenophases were explained mainly by relative humidity, and reproductive phenophases by relative humidity and temperature. Analyzing the plant species separately, *B. campestris* and *B. verbascifolia* were more influenced by relative humidity, which explained four of their phenophases. *H. umbellata* and *P. tomentosa* were more influenced by temperature, which explained three and four of their phenophases, respectively.

Specific sets of abiotic variables significantly influenced the phenophases of the studied species ($P < 0.05$). In *B. campestris*, the photoperiod positively influenced the production of new leaves ($R^2 = 0.326$). The phenophase of mature leaves was negatively related to photoperiod and positively related to relative humidity ($R^2 = 0.392$). The leaf falling was positively related to photoperiod and negatively related to temperature and relative humidity, which explained 76.7% of the variation. Flower bud phenophase had no significant relationship with any climatic variable (all $P > 0.05$). Relative humidity explained 17.1% of flower production, in a positive relationship. Finally, fruiting was explained negatively by precipitation and positively by temperature and relative humidity, which explained 40.3% of fruit production (Figure 2 and Table S2, Suplementary Material S1).

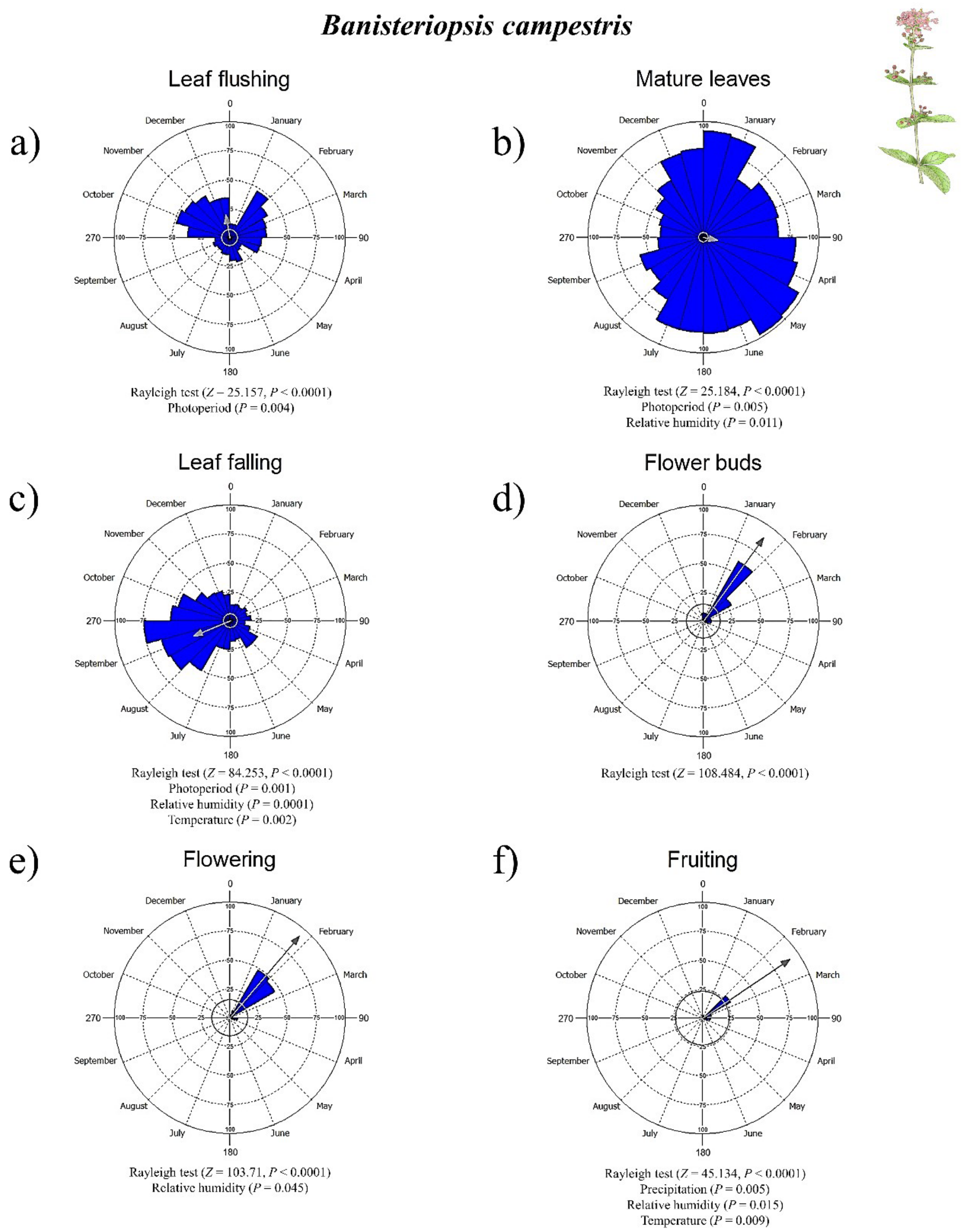

Figure 2. Circular histograms showing the intensity of individuals of *Banisteriopsis campestris* in each phenological event, between January and December 2017, in the cerrado *sensu stricto* of the Serra de São José Environmental Protection Area, Tiradentes, MG, Brazil. (a) leaf flushing, (b) mature leaves, (c) leaf falling, (d) flower buds, (e) flowering, and (f) fruiting. The arrows point to the angle of the mean vector (µ) and its size represents the length of mean vector (r). Below each figure is the result of the Rayleigh (Z) test for circular uniformity, as well as the climatic variables that interfered in the triggering of the phenophases.

For *B. verbascifolia*, the production of new leaves was explained negatively by precipitation, and positively explained by relative humidity ($R^2 = 0.323$). Temperature showed a negative relationship with the occurrence of mature leaves, explaining 20.4% of the variation. Leaf falling was positively predicted by photoperiod and negatively predicted by relative humidity ($R^2 = 0.468$). None of the climatic variables studied explained the production of flower buds ($P > 0.05$). Flowering was positively predicted by photoperiod and negatively predicted by temperature

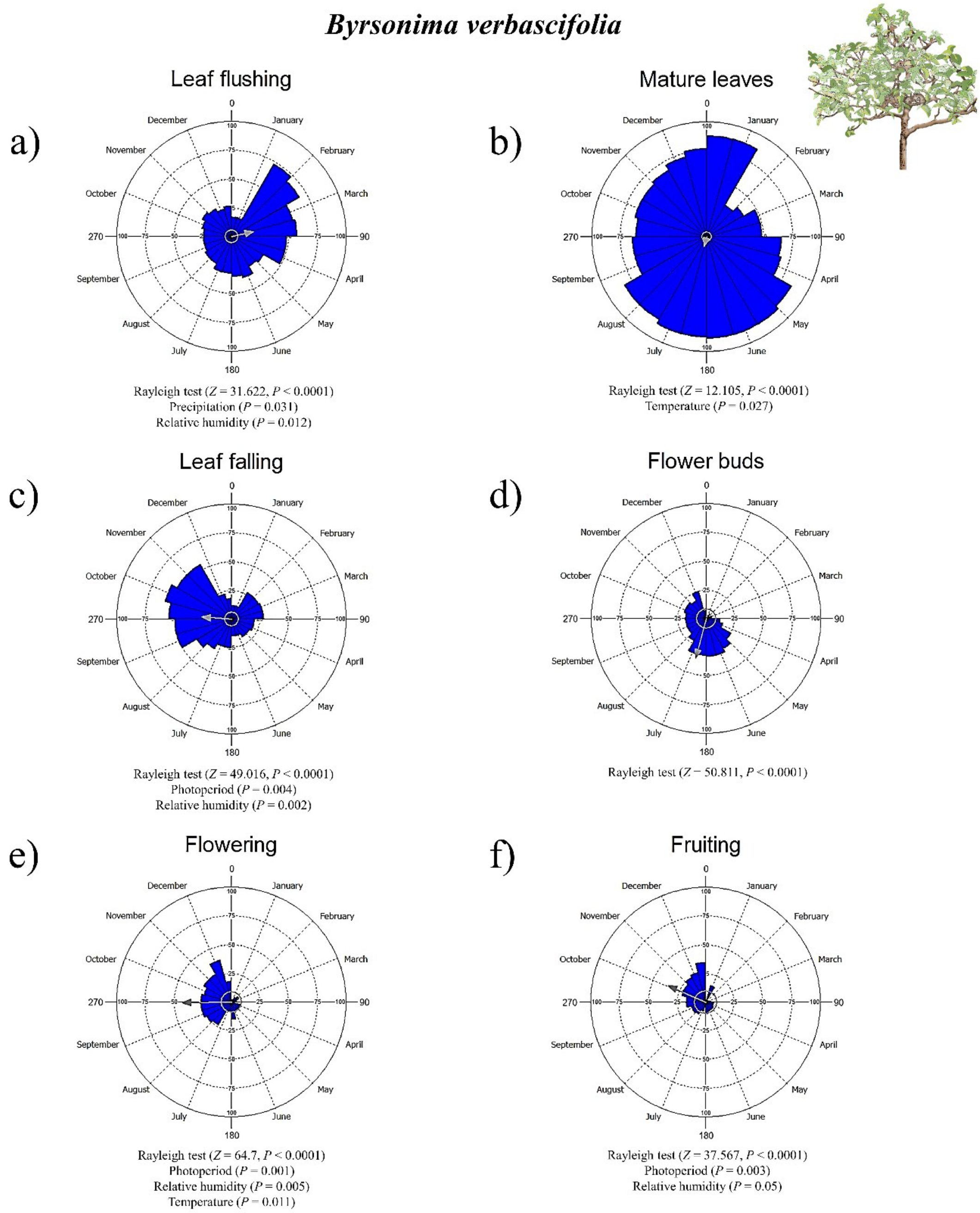

Figure 3. Circular histograms showing the intensity of individuals of *Byrsonima verbascifolia* in each phenological event, between January and December 2017, in the cerrado *sensu stricto* of the Serra de São José Environmental Protection Area, Tiradentes, MG, Brazil. (a) leaf flushing, (b) mature leaves, (c) leaf falling, (d) flower buds, (e) flowering, and (f) fruiting. The arrows point to the angle of the mean vector (μ) and its size represents the length of mean vector (r). Below each figure is the result of the Rayleigh (Z) test for circular uniformity, as well as the climatic variables that interfered in the triggering of the phenophases.

and relative humidity, which explained 47% of the variation. Finally, the photoperiod and relative humidity explained 40.9% of fruit production, in a positive and negative relationship with this phenophase, respectively (Figure 3 and Table S2, Suplementary Material S1).

Temperature explained 23.8% of leaf production in *H. umbellata*, having a positive relationship with phenophase. Temperature and relative humidity positively relate to the phenophase of mature leaves ($R^2 = 0.625$). These same explanatory variables explained 60% of leaf fall,

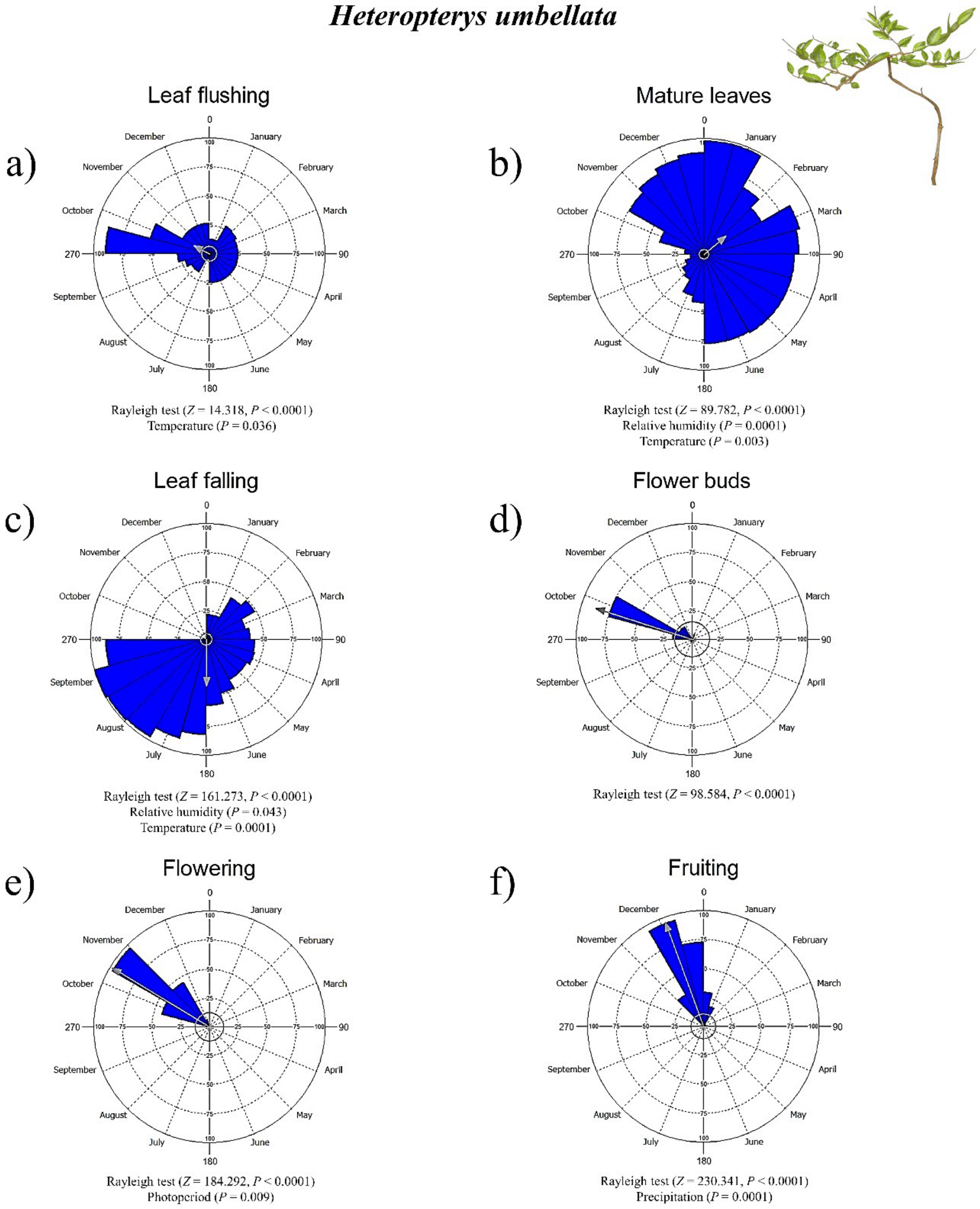

Figure 4. Circular histograms showing the intensity of individuals of *Heteropterys umbellata* in each phenological event, between January and December 2017, in the cerrado *sensu stricto* of the Serra de São José Environmental Protection Area, Tiradentes, MG, Brazil. (a) leaf flushing, (b) mature leaves, (c) leaf falling, (d) flower buds, (e) flowering, and (f) fruiting. The arrows point to the angle of the mean vector (µ) and its size represents the length of mean vector (r). Below each figure is the result of the Rayleigh (Z) test for circular uniformity, as well as the climatic variables that interfered in the triggering of the phenophases.

both with a negative relationship with the phenophase. The climatic variables tested did not explain the production of flower buds ($P > 0.05$). Photoperiod showed a positive relationship with flowering ($R^2 = 0.282$). Finally, fruit production was positively predicted by precipitation ($R^2 = 0.441$) (Figure 4 and Table S2, Suplementary material S1).

P. tomentosa had no significant relationship with climatic variables for leaf flushing phenophase ($P > 0.05$). The phenophase of mature leaves was negatively predicted by photoperiod and positively predicted by temperature and relative humidity ($R^2 = 0.538$). The leaf falling was positively predicted by photoperiod and negatively by

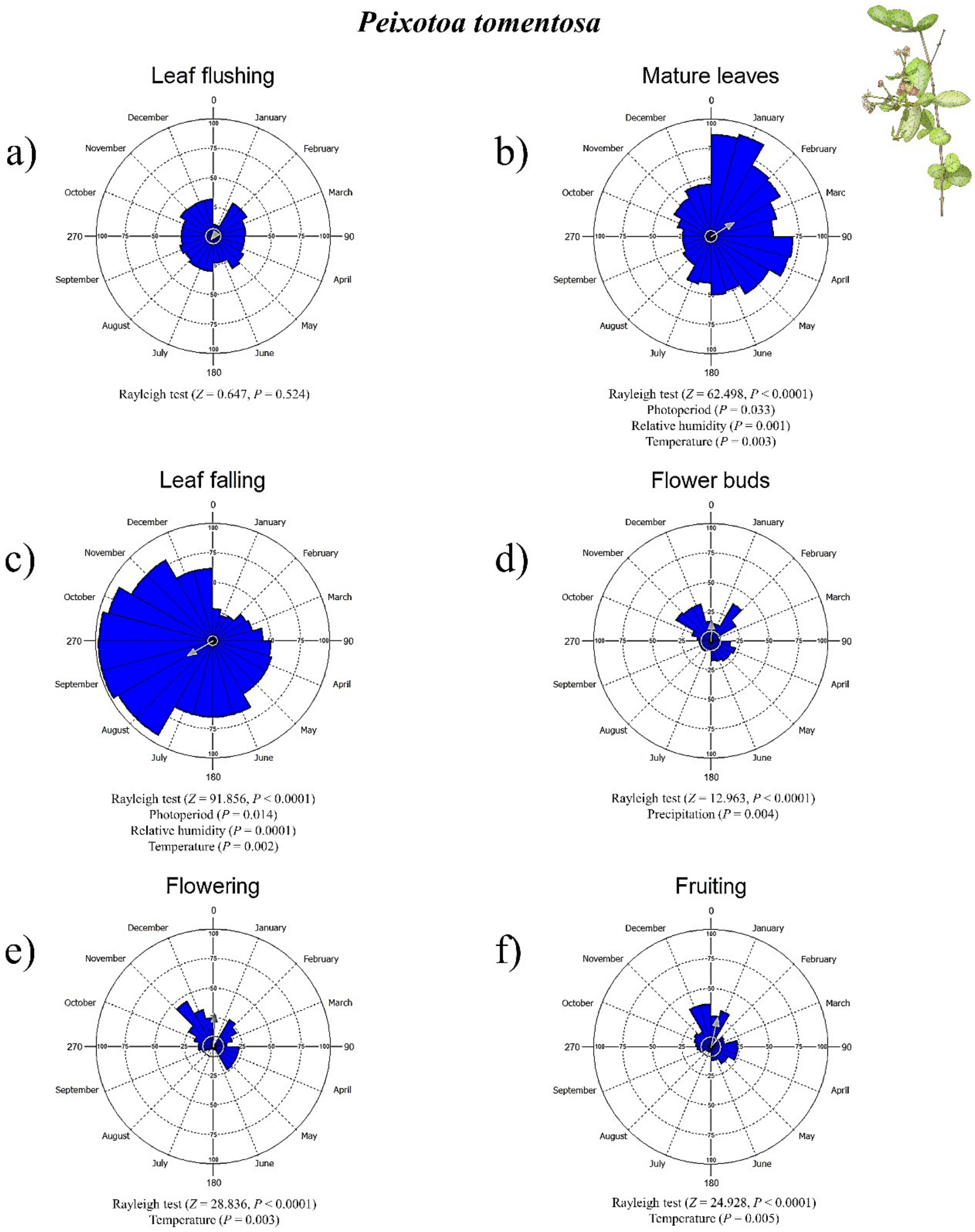

Figure 5. Circular histograms showing the intensity of individuals of *Peixotoa tomentosa* in each phenological event, between January and December 2017, in the cerrado *sensu stricto* of the Serra de São José Environmental Protection Area, Tiradentes, MG, Brazil. (a) leaf flushing, (b) mature leaves, (c) leaf falling, (d) flower buds, (e) flowering, and (f) fruiting. The arrows point to the angle of the mean vector (μ) and its size represents the length of mean vector (*r*). Below each figure is the result of the Rayleigh (*Z*) test for circular uniformity, as well as the climatic variables that interfered in the triggering of the phenophases.

temperature and relative humidity, which explained 62.4% of leaf fall. Precipitation showed a positive relationship with the production of flower buds (R^2 = 0.315). Finally, temperature showed a positive relationship with the production of flowers and fruits, explaining 33.5% and 31.1% of these phenophases, respectively (Figure 5 and Table S2, Suplementary Material S1).

4. Discussion

Our findings show that plant species of the Malpighiaceae family produced new leaves over the two seasons, with an intense leaf falling in the dry season, and their flowering did not overlap, presenting a sequential and asynchronous flowering pattern among their individuals. Our results also

Table 1. Results of circular analyses for seasonal patterns in the vegetative and reproductive phenophases of the four plant species of the Malpighiaceae family studied between January and December 2017 in the cerrado *sensu stricto* of the Serra de São José Environmental Protection Area, Tiradentes, MG, Brazil.

Species/ Phenophases	Number of Observations	Rayleigh test (*Z*)	Rayleigh test (*P*)	Mean vector (μ)	Date	Median	Standard Error of Mean	Length of mean vector (*r*)
Banisteriopsis campestris								
Leaf flushing	622	25.157	0.0001*	350.378°	December/2	345°	7.994°	0.201
Mature leaves	1671	25.184	0.0001*	101.072°	April/1	105°	8.043°	0.123
Leaf falling	722	84.253	0.0001*	247.398°	September/1	255°	4.279°	0.342
Flower buds	139	108.484	0.0001*	35.919°	February/1	30°	2.414°	0.883
Flowering	121	103.71	0.0001*	40.403°	February/1	45°	2.043°	0.926
Fruiting	55	45.134	0.0001*	55.917°	February/2	45°	3.43°	0.906
Byrsonima verbascifolia								
Leaf flushing	847	31.622	0.0001*	77.058°	March/2	75°	7.136°	0.193
Mature leaves	1700	12.105	0.0001*	196.592°	July/2	210°	11.624°	0.084
Leaf falling	721	49.016	0.0001*	274.373°	October/1	285°	5.686°	0.261
Flower buds	414	50.811	0.0001*	195.389°	July/2	195°	5.501°	0.350
Flowering	356	64.7	0.0001*	269.503°	September/2	270°	4.792°	0.426
Fruiting	293	37.567	0.0001*	294.03°	October/2	300°	6.387°	0.358
Heteropterys umbellata								
Leaf flushing	628	14.318	0.0001*	298.193°	October/2	285°	10.645°	0.151
Mature leaves	1493	89.782	0.0001*	49.907°	February/2	60°	4.21°	0.245
Leaf falling	1032	161.273	0.0001*	180.189°	July/1	180°	3.058°	0.395
Flower buds	131	98.584	0.0001*	287.825°	October/2	285°	2.661°	0.867
Flowering	192	184.292	0.0001*	301.224°	November/1	300°	0.837°	0.980
Fruiting	254	230.341	0.0001*	339.76°	December/1	330°	1.124°	0.952
Peixotoa tomentosa								
Leaf flushing	665	0.647	0.5244	219.772°	August/1	195°	50.369°	0.031
Mature leaves	1184	62.498	0.0001*	58.762°	February/2	60°	5.056°	0.230
Leaf falling	1508	91.856	0.0001*	240.022°	September/1	240°	4.161°	0.247
Flower buds	424	12.963	0.0001*	1.187°	January/1	15°	11.165°	0.175
Flowering	364	28.836	0.0001*	1.559°	January/1	345°	7.39°	0.281
Fruiting	387	24.928	0.0001*	13.347°	January/1	0°	7.98°	0.254

* = indicates statistically significant results at $P < 0.05$.

showed that the phenological patterns of the four plant species evaluated are directly linked to climatic variables, where different abiotic factors are more important than others to explain the expression of each phenophase.

We observed that the vegetative and reproductive phenophases were mainly conditioned by relative humidity and temperature, respectively. In the rainy season, most plants generally grow better, free from stressful conditions in this environment, such as water stress and low temperatures (Borchert, 1999; O'Brien et al., 2008; Lacerda et al., 2018). Consequently, most phenophases were positively related to these climatic variables at that time of year. However, leaf fall of species, in general, had a negative relationship with climatic variables in the dry season. That is, lower temperatures were associated with leaf fall of *B. campestris*, *H. umbellata*, and *P. tomentosa* and the decrease in relative humidity in the dry season influenced the leaf fall of all species, corroborating the predicted pattern for this seasonal environment (Williams et al., 1997; Morellato et al., 2016).

The intensity index revealed that leaf production occurred over the two seasons for all studied species. Leaf flushing of the species showed peak intensity in the rainy season and, in the dry season, there was a higher decrease in young leaves. According to Borchert (1999), this pattern is commonly observed in seasonal environments, in which lower rainfall and humidity, and increased temperatures at the end of the dry season are physiological triggers for abscission. In addition, the decrease in leaf production in the species coincided with fruit maturation, suggesting a reallocation of resources deviated from vegetative to reproductive development (Munhoz and Felfili, 2005; Novaes et al., 2020).

The leaf falling was more intense for all species at the end of the dry season, with few leaves falling the rest of the year, which is in line with expectations for an environment with seasonal water restrictions (Kikuzawa, 1991; Munhoz and Felfili, 2005), in addition to illustrating the water stress escape mechanism (O'Brien et al., 2008). That is, in the absence of rain and the presence of heat and wind, leaf falling can help conserve water, preventing the plant's vital activities from being compromised in the dry season (Goldstein et al., 2008). As for the deciduousness of the plants, *H. umbellata* and *P. tomentosa* presented brevideciduous behavior in the studied area, losing all their leaves in a period shorter than 21 days (Lenza and Klink, 2006; Araújo and Haridasan, 2007).

The phenophase of flower buds and flowering occurred throughout the year for *P. tomentosa* and *B. verbascifolia*, presenting a continuous pattern (Newstrom et al., 1994), but with intensity peaks in the rainy season. This pattern can be explained by the self-incompatibility of these species, that is, they are less pollen-limited and less dependent on pollinators, being able to flower at different times of the year (Rodger and Ellis, 2016). On the other hand, *B. campestris* presented flower buds and flowers throughout the rainy season, showing an annual pattern of flowering (Newstrom et al., 1994). *H. umbellata*, on the other hand, presented a minimum production of flower buds in the dry season, not generating flowers and fruits, but this evidences a possible sub-annual pattern for the reproductive phenophases.

The studied plant species presented a spatiotemporal organization of their floral resources. Although *B. verbascifolia* and *P. tomentosa* produce flowers throughout the year, their intensity peaks did not overlap, either with the other two species studied, which presented annual flowering, evidencing a sequential flowering pattern in the studied area (see Table 1) (Gentry, 1974). The sequential flowering of sympatric species generates the conditions necessary for the maintenance of pollinators and maximizes intraspecific pollen transfer (LaFrankie and Chan, 1991; Vilela et al., 2014), having been described for the Malpighiaceae family in previous studies (see Sigrist and Sazima, 2004; Costa et al., 2006; Torezan-Silingardi, 2007; Vilela et al., 2014). Sequence flowering can be triggered by climatic factors such as temperature, photoperiod, and precipitation (Gentry, 1974; Rathcke and Lacey, 1985; Vilela et al., 2014), and, according to Gentry (1974), it can be the result of selective pressure exerted by competition by pollinators in sympatric species of the same family. These species also exhibited a spatiotemporal organization of their flowers among individuals in their populations. Thus, the asynchronous flowering exhibited among individuals of the studied species may be related to a selective pressure exerted by intraspecific competition (Rathcke and Lacey, 1985). As few plants flower at the same time, this mechanism can guarantee that a higher number of flowers can be visited (Waser et al., 1996). Thus, floral asynchrony maintains flowers in the population over a longer time, favoring opportunistic pollinators and providing a higher rate of cross-pollination. Furthermore, this strategy can increase the pollination of various plants in a possible seasonal insect deficiency (Waser et al., 1996).

Despite being anemochoric, *B. campestris* and *H. umbellata* did not fruit in the dry season, and *P. tomentosa*, which produced fruits throughout the year, had no peak intensity at that time. We suggest that the fruiting peaks of these species must be linked to the synchronization of germination with the beginning of the rainy season, which would increase the chances of seedling survival (Mendoza et al., 2017). The fruiting of *B. verbascifolia*, with few fruits offered throughout the year, on the other hand, maybe the result of an evolutionary strategy to increase its dispersion. Subannual production could offset the low investment in fruit production, attracting generalist frugivores, who would consume their fruit in periods when other species are not fruiting (Schupp et al., 2010; Kuhlmann and Ribeiro, 2016).

We show here a very close relationship between climatic variables and the phenophases of the studied plant species. Thus, we suggest that global warming may alter the phenology of these plant species studied here. Several studies have evaluated and shown the importance of climatic variables in plant ecology in the Brazilian savanna (Vilela et al., 2017; Novaes et al., 2020). Vilela et al. (2017) reported that the variation in precipitation and temperature in the Cerrado over ten years affected the flowering period of the plants, interfering with the interaction with pollinators. In fact, climate stability is a key factor that regulates the availability of resources for fauna (Abrahamczyk and Kessler, 2015). In this sense, predicted changes in spatiotemporal patterns of vegetative and reproductive phenology can be a threat to interactions because guilds of herbivores, pollinators and dispersers are structured by spatial and temporal variation in the diversity of resources (Burkle and Alarcon, 2011, Carstensen et al., 2014). If, in fact, many species are becoming asynchronous (McKinney et al., 2012), this further emphasizes the need to take measures to reduce climate change, as the effects can be detrimental to species persistence (Visser and Both, 2005), especially for species with specialized interactions (Memmott et al., 2007). Thus, quantifying these impacts on biodiversity and formulating measures capable of minimizing them represent major challenges for research in the coming decades.

Our findings are of great importance for understanding the phenology of plants from seasonal tropical environments, the spatiotemporal organization of available resources, and show the importance of climatic variables on triggering phenological events.

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Supplementary Material

Supplementary material accompanies this paper.

Supplementary Material S1: Influence of climatic seasonality on sympatric species of Malpighiaceae Juss. on a tropical savanna. **Table S1.** Average values of photoperiod, relative humidity, and temperature, and accumulated values of precipitation over the 24 fortnights of 2017 in the cerrado *sensu stricto* of the São José Environmental Protection Area, Tiradentes, MG, Brazil. **Table S2.** Generalized Linear Models (GLMs) showing the relationship between climatic variables and phenophases of the studied Malpighiaceae plant species. Rel = Relationship, + positive relationship, − negative relationship, / no relationship.

Supplementary Material S2: Influence of climatic seasonality on sympatric species of Malpighiaceae Juss. on a tropical savanna. **Figure S1.** Percentage of individuals (activity) of *Banisteriopsis campestris* that expressed vegetative and reproductive phenological events from January to December 2017 in the cerrado *sensu stricto* of the São José Environmental Protection Area, Tiradentes, MG, Brazil. **Figure S2.** Percentage of individuals (activity) of *Byrsonima verbascifolia* that expressed vegetative and reproductive phenological events from January to December 2017 in the cerrado *sensu stricto* of the São José Environmental Protection Area, Tiradentes, MG, Brazil. **Figure S3.** Percentage of individuals (activity) of *Heteropterys umbellata* that expressed vegetative and reproductive phenological events from January to December 2017 in the cerrado *sensu stricto* of the São José Environmental Protection Area, Tiradentes, MG, Brazil. **Figure S4.** Percentage of individuals (activity) of *Peixotoa tomentosa* that expressed vegetative and reproductive phenological events from January to December 2017 in the cerrado *sensu stricto* of the São José Environmental Protection Area, Tiradentes, MG, Brazil.

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