

Original Article

Effects of ENSO events on the intensity, seasonality, and diversity of reproductive phenology of *Miconia* (Melastomataceae) species in tropical rainforest

Efeitos de eventos ENOS sobre a intensidade, sazonalidade e diversidade da fenologia reprodutiva de espécies de *Miconia* (Melastomataceae) em floresta tropical úmida

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Abstract

We evaluated the phenology and reproductive phenological diversity of three sympatric species of *Miconia* in a gallery forest in the Chapada Diamantina mountains, Bahia, Brazil. The reproductive phenophases (bud, flower, immature fruit, and mature fruit) of *M. alborufescens* (N=38), *M. holosericea* (N=46), and *M. prasina* (N=44) were evaluated monthly, between June/2008 and June/2015. The Fournier index was used to assess the intensities of the reproductive phenophases; synchrony and seasonality were analyzed using circular statistics and the Rayleigh (Z) test. The Frideman and Wilcoxon tests were used to verify interannual variations in phenological patterns. Reproductive phenological diversity was measured by calculating the Shannon-Wiener index; ANOVA tested possible differences in the means of diversity among the different years. The reproductive phenophases of the studied *Miconia* species occurred sequentially (*M. alborufescens*, then *M. holosericea*, followed by *M. prasina*), in the transition between the dry and rainy seasons, with little overlap between them. In general, the species showed seasonal and synchronic phenological patterns, with some variations that coincided with El Niño and/or La Niña events, e.g., demonstrating changes in the periodicity, synchrony, and intensity of their phenophases. The intensity of fruiting, for example, showed increases during La Niña years. Reproductive phenological diversity appears to respond to climate changes resulting from El Niño events and periods of prolonged drought, with high Shannon-Wiener index values. The results also suggest that the effects of global climatic phenomena (El Niño and La Niña) that alter regional climatic seasonality can also cause variations in the reproductive phenological rhythms of the *Miconia* species studied.

Keywords: climatic changes, El Niño, La Niña, phenological diversity, sequential flowering.

Resumo

Neste estudo, avaliamos a fenologia e a diversidade fenológica reprodutiva de três espécies simpátricas de *Miconia* em uma floresta de galeria da Chapada Diamantina, Bahia, Brasil. As fenofases reprodutivas (botão, flor, fruto imaturo e fruto maduro) de *M. alborufescens* (N=38), *M. holosericea* (N=46) e *M. prasina* (N=44) foram avaliadas mensalmente, entre junho de 2008 e junho de 2015. O índice de Fournier foi utilizado para avaliar a intensidade das fenofases reprodutivas; a sincronia e a sazonalidade foram analisadas por meio de estatística circular e do teste de Rayleigh (Z). Os testes de Frideman e Wilcoxon foram empregados na verificação de variações interanuais dos padrões fenológicos. A diversidade fenológica reprodutiva foi mensurada pelo cálculo do índice de Shannon-Wiener; a ANOVA testou possíveis diferenças nas médias de diversidade entre os diferentes anos. As fenofases reprodutivas das espécies de *Miconia* estudadas ocorreram de forma sequencial (*M. alborufescens*, *M. holosericea* e *M. prasina*, respectivamente), na transição entre as estações seca e chuvosa, com pouca sobreposição entre as espécies. No geral, as espécies apresentaram padrões fenológicos sazonais e sincrônicos, com algumas variações que coincidiram com eventos de El Niño e/ou La Niña, e.g., demonstrando mudanças na periodicidade, sincronia e intensidade de suas fenofases. A intensidade da frutificação, por exemplo, apresentou aumento nos anos de ocorrência de La Niña. A diversidade fenológica reprodutiva parece responder às alterações climáticas decorrentes dos eventos de El Niño e a períodos de seca prolongada, com valores elevados do índice de Shannon-Wiener. Os resultados sugerem, ainda, que os efeitos de fenômenos climáticos globais (El Niño e La Niña), que alteram a sazonalidade climática regional, também podem causar variações nos ritmos fenológicos reprodutivos das espécies de *Miconia* estudadas.

Palavras-chave: mudanças climáticas, El Niño, La Niña, diversidade fenológica, floração sequencial.

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1. Introduction

Plant reproductive phenology is key to understanding how flowering and fruiting episodes are related to environmental and biotic factors, in light of their crucial importance to plant reproductive success (Macfarlane, 2021; Pereira et al., 2024). Rainfall, photoperiod, and temperature variations have been identified as the main triggers of flowering and fruiting events in tropical forests (Brito et al., 2017; Souza and Funch, 2017). In seasonal environments, climate can affect spatiotemporal variations of flower and fruit production (van Schaik et al., 1993; Morellato et al., 2016) and, consequently, interactions with pollinators and dispersal agents that are directly responsible for its reproductive success (Brito et al., 2017). It is therefore expected that climate change will provoke changes in the season, duration, intensity, and periodicity of flower and fruit production (Nhongo et al., 2017). The reproductive seasonality of plant species pollinated and dispersed by animals has been well documented (Brito et al., 2017; Renton et al., 2018), although the effects of global climatic phenomena (e.g. El Niño and La Niña) on the seasonality and synchrony of the reproductive phenology of plant populations growing in tropical forests are still poorly known (Sakai and Kitajima, 2019; Davis et al., 2022).

The flowering and fruiting dynamics of plants can be analyzed by monitoring species over long periods and then comparing their phenological responses in different years (Wright et al., 2019). The analysis of phenological variability within populations can provide information on their potential resilience to changing climatic conditions (Davis et al., 2022). Studies on phenological diversity in tropical ecosystems have largely focused on spatial comparisons of plant populations subjected to very different environmental conditions, especially in terms of water availability (humid forests *versus* seasonally dry forests), although they have generally considered only short time series (≤ 2 years) (Goulart et al., 2005; Santos et al., 2020; Costa et al., 2021). Long-term series are important tools for characterizing phenological patterns (Macfarlane, 2021) and can aid investigations into how plants will respond to climate change (Sakai and Kitajima, 2019; Davis et al., 2022), especially in highly diverse and phenologically heterogeneous tropical systems (Morellato et al., 2016). Phenological rhythms in tropical regions are susceptible to the effects of global climatic phenomena such as the El Niño/La Niña Southern Oscillation (ENSO) that affects rainfall patterns and tends to cause alternating drought and increased rainfall events (Menezes et al., 2017).

Melastomataceae is a pantropical plant family comprising 1,430 species in Brazil that occur in all of its phytogeographic domains (Dellinger et al., 2022). *Miconia* is the genus of this family with the highest number of species (Meyer, 1998), and its abundance in the humid forests of the Chapada Diamantina mountains (Funch et al., 2008) indicates its regional ecological importance of offering flower and fruit resources to floral visitors and frugivorous/dispersers. Brito et al. (2017) analyzed the reproductive phenology of 81 species of Melastomataceae growing in the Atlantic Forest and campo rupestre vegetation in Brazil and demonstrated that, at the family level, flowering can

be influenced by different reproductive strategies, while fruiting patterns mainly reflect seed dispersal strategies and flowering times, with less phylogenetic influence.

We therefore investigated the seasonality and diversity patterns of the flowering and fruiting of three sympatric species of melittophilic and ornithochoric *Miconia* growing in gallery forests in the Chapada Diamantina mountains in northeastern Brazil. Based on a seven-year time series, we sought to address the following questions: (i) Do the reproductive phenological rhythms of the *Miconia* species studied reflect regional climatic seasonality? (ii) Are there significant interannual variations in the reproductive phenology of these species related to El Niño/La Niña events? As seasonal blooms of melittophilous and zoochorous species have been associated with higher bee abundance and greater richness of both pollinators and dispersers during warm and rainy seasons (Hoiss et al., 2012; Silveira et al., 2013) and *Miconia* species are known to produce fleshy fruits that are rich in sugar and require abundant water availability (Silveira et al., 2013), we hypothesize that the reproductive phenologies of *Miconia* species will be seasonal (Funch et al., 2002), with flowering at the end of the dry season or early rainy season, with fruiting during the rainy season. We also expect that the temporal variation associated with ENSO will affect the duration, periodicity, and intensity of the reproductive phenophases of those species (Cleland et al., 2007; Chang-Yang et al., 2016; Chapman et al., 2018).

2. Material and Methods

2.1. Study area and target species

The Chapada Diamantina mountains in northeastern Brazil hold a rich mosaic of vegetation types, with evergreen forests growing along riversides and on mountain slopes (Funch et al., 2009). Our study was conducted in a gallery forest of the Lençóis River (12°33'38.6" to 12°33'23.1" S and 41°24'10.7" to 41°24'40" W) (Figure 1a-b) that occupies a relatively narrow strip of land (varying from 15 to 25 m wide) parallel to the river on dystrophic litholic soils at altitudes between 400 m and 500 m. Soil moisture levels vary between 75% and 16% during the rainy and dry seasons, respectively (Miranda et al., 2011). The upper canopy of this gallery forest is formed by trees up to 10 m tall, with some emergent individuals up to 20 m tall; the discontinuous sub-canopy, ranging in height from 3.5 m to 8.0 m, includes several species of Melastomataceae (Funch et al., 2008). The region has a tropical climate (Aw, according to the Köppen system) with an average monthly rainfall of 100 mm (Figure 1c), a rainy season concentrated in the Austral summer (December–April), and a dry winter season (July–August) (Alvares et al., 2013) (Figure 1d-e). The mean monthly precipitation generally varies from 35 mm (July and August) to 184 mm (December), with the total mean annual precipitation varying from 700 mm to 1,300 mm. Mean monthly temperatures vary between 18 °C (April–September) and 22 °C (October–February) (Alvares et al., 2013).

We studied three melittophilous and ornithochorous shrub-tree species *Miconia* species, which together

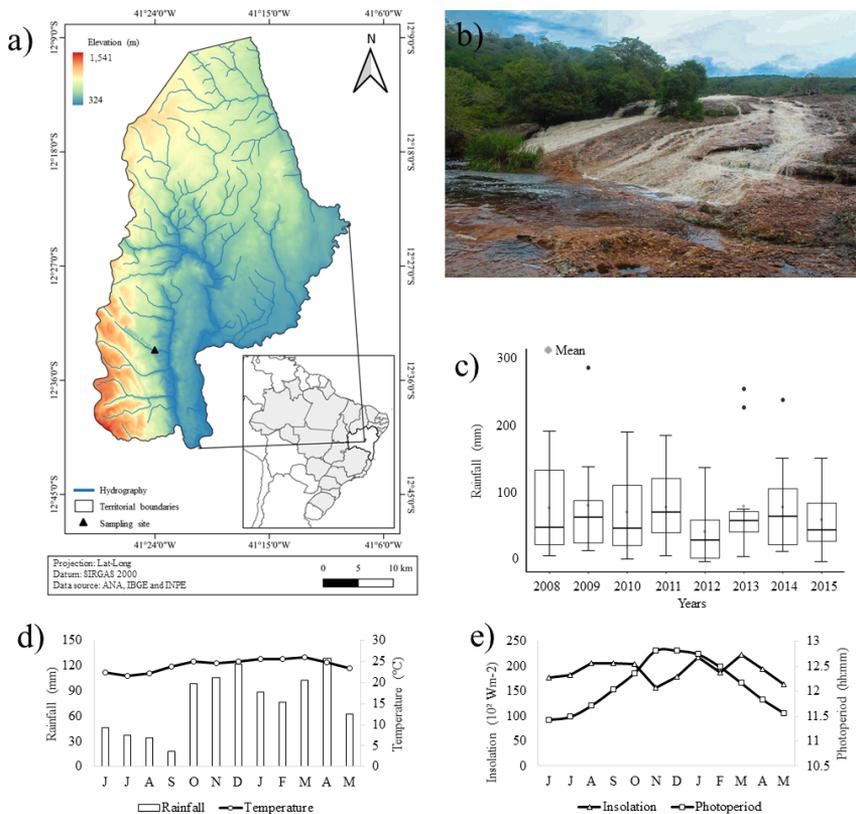


Figure 1. Chapada Diamantina, Bahia, Brazil. (a) Hydrography and elevation of the municipality of Lençóis; (b) gallery forest of the Lençóis River; (c) average annual precipitation between June/2008 and May/2015; (d) monthly rainfall and temperature averages during 2008–2015; and (e) monthly means of insolation and photoperiod for the years 2008–2015.

represent 13% of the sub-canopy species of the gallery forest (Funch et al., 2008): *M. alborufescens* Naud. (HUEFS 158701); *M. holosericea* (L.) DC. (HUEFS 260193); and *M. prasina* (Sw) DC. (HUEFS 254696). These species are not endemic to Brazil but are widely distributed in the Amazon, Caatinga, Cerrado, and Atlantic Forest domains (Dellinger et al., 2022). Species vouchers were deposited in the State University of Bahia at Feira de Santana Herbarium (HUEFS). *Miconia alborufescens* is a shrub 1–3 m tall, with inflorescences in panicles of glomeruli; pentamerous flowers; corolla, stamens, and anthers white and uniporous; berry-type fruit, red when immature and black when mature (Figure 2a). *Miconia holosericea* is a small tree 3–6 m tall, with inflorescences in panicles of terminal glomeruli; hexamerous flowers, white corolla, and pink nuances at the base of the petals; white stamens, and lilac uniporous anthers; immature fruits are green berries, the mature fruits are black (Figure 2b). *Miconia prasina* is a tree up to 8 m tall, with inflorescences in terminal panicles; pentamerous flowers, corolla, stamens, and anthers white, uniporous; immature fruits are green berries and mature fruits are black (Figure 2c).

2.2. Environment variables

Climatic data were obtained from Lençóis Meteorological Station, maintained by the National Institute of Meteorology

(INMET – <https://bdmep.inmet.gov.br/>). Photoperiod data were obtained from the US Naval Observatory's Department of Astronomical Applications website (http://aa.usno.navy.mil/data/docs/RS_OneYear.php).

Northeastern Brazil experiences significant interannual variations of total rainfall, partially due to ENSO. El Niño events alter the global climate by modifying rainfall patterns in tropical and semitropical regions, with northeastern Brazil experiencing reduction in cloud cover and rainfall (Marengo et al., 2011). The Oceanic Niño Index (ONI) consists of positive values for the El Niño warm phase and negative values for the La Niña cold phase. According to ONI values obtained from the National Oceanic and Atmospheric Administration (NOAA, 2023) two El Niño and four La Niña occurrences were recorded during the study period (Table S1, Supplementary Material 1).

2.3. Reproductive phenology

This study was performed using unpublished phenological datasets for *Miconia* species that were collected by our research group during previous work in the gallery forest along the Lençóis River. Phenological information gathered from 128 tagged shrub-tree species of *Miconia* was evaluated: *M. alborufescens* (38 individuals), *M. holosericea* (46), and *M. prasina* (44). Data collection was



Figure 2. Phenology of three sympatric species of *Miconia* growing in a tropical forest on the Lençóis River, Chapada Diamantina, northeastern Brazil. Arranged from right to left: floral buds, flowers, immature fruits, and mature fruits of (a) *Miconia alborufescens*; (b) *M. holosericea*; and (c) *M. prasina*.

carried out between 2008 and 2015, totaling 85 months of observations. Our observations occurred at mean interval of 30 days, near the end of each month. The reproductive phenophases monitored were the production of floral buds, flowers, and immature and mature fruits. Data collection was based on a qualitative methodology – the presence or absence of a given phenophase, and on a semi-quantitative methodology (Fournier, 1974) – estimating the intensity of each phenophase using a scale with five categories (0 to 4), at 25% intervals. We evaluated reproductive phenological patterns based on their frequencies (number of cycles per unit time – continual: continuous flowering or few brief interruptions; subannual: > 1 cycle per year; annual: 1 cycle per year; and supra-annual: multi-year cycles), durations (length of time a unit remains in a given portion of the cycle – brief: < 1 month; intermediate > 1 month and < 5 months; and extended: > 5 months), and regularities (variability in length of cycles or portions of the cycles) of the seasons (Newstrom et al., 1994).

2.4. Data analysis

The seasonalities of the phenological data of flowering and fruiting were analyzed based on circular statistics, in which the months of the year were converted into 30° angle intervals (Morellato et al., 2010). For each phenophase, we calculated: (i) the mean angle, which represents the mean date of the phenological activity considered; (ii) the length of the r vector, which reflects the aggregation of the dates (event synchrony), and the seasonality of the species studied (r values > 0.5 indicating aggregation/seasonality of the phenological event); and performed (iii) the Rayleigh test (z) to determine if the dates demonstrated

uniform distributions throughout the year (Zar, 2010). The null hypothesis (H_0) would indicate that the angles (dates) were uniformly distributed throughout the year, i.e., there was no seasonality. On the other hand, if H_0 is rejected, the phenophase patterns would be seasonal (Morellato et al., 2010). All of the circular analyses were performed using the “circular” package of R software, version 4.0.2 (R Core Team, 2020). The Friedman and Wilcoxon signed-rank classification tests were used to assess interannual reproductive variations of phenological events, and whether they were repeated in subsequent years (Morellato et al., 2010; Zar, 2010), using the R software, version 4.0.2. (R Core Team, 2020).

We evaluated the reproductive phenological diversity of each species using the Fournier categories. The individuals were characterized according to the combinations of their categories (0, 1, 2, 3, and 4) that corresponded to observed phenophases and were classified as reproductive “phenological states”. After the characterization of each sampled individual, phenological diversity was estimated using the Shannon–Wiener Index (adapted) (Goulart et al., 2005; Santos et al., 2020; Costa et al., 2021), considering the equation proposed by Magurran (1988). In practice, the values assigned by the Shannon–Wiener Index are usually between 1.5 and 3.5 (but can reach 4.5), with low values indicating low diversity (Magurran, 1988). Reproductive phenological diversity data for each species were tested using analysis of variance (ANOVA) to verify whether their mean values were significantly different within populations ($P < 0.05$) over the seven study years. The tests were performed using R software, version 4.0.2. (R Core Team, 2020).

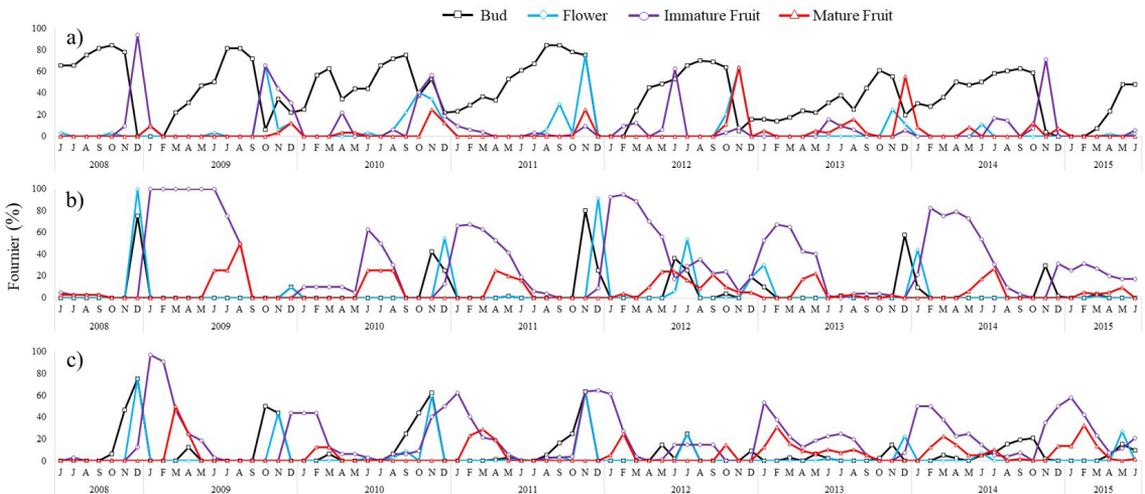


Figure 3. Reproductive phenology of three species of *Miconia* growing in a tropical forest on the Lençóis River, Chapada Diamantina, northeastern Brazil. (a) *Miconia alborufescens*; (b) *M. holosericea*; and (c) *M. prasina*. The letters on the horizontal axis correspond to the months in each year of study.

3. Results

3.1. Pattern, seasonality, and diversity of the reproductive phenology of *M. alborufescens*

Flowering exhibited an annual pattern, brief to intermediate (1–5 months), irregular, and associated with the transition season (dry–raining), between August and December, with lower productivity than budding (Figure 3a). The production of flower buds was continuous, and remained high (up to 80% Fournier intensity), although with three brief interruptions during the study period. The fruiting pattern is annual, intermediate, and regular (Figure 3). Immature and mature fruits showed intensity peaks at the beginning of the rainy season, from October to December. The reproductive phenophases flower, immature fruit, and mature fruits were seasonal and synchronous, except between 2011–12, and flower buds were aseasonal and asynchronous during most of the study; the mean dates of flowering occurred between July and October, while fruiting varied between October and May (Table 1).

M. alborufescens showed interannual variations in its phenological patterns that coincided with the occurrence of ENSO events, such as the production of flower buds in 2014–15 (El Niño) and mature fruits between 2008–09 and 2009–10 (La Niña and El Niño respectively) (Table S2, Supplementary Material). The reproductive phenological diversity of *M. alborufescens* was varied and high (Figure 4a), with a total mean of 1.1 ± 0.5 for the study period (see Figure S1, Supplementary Material for annual means). There was a decrease in diversity in January (0.7 ± 0.7) and February (0.6 ± 0.7), and an increase in diversity in November (1.4 ± 0.5). The highest diversity was recorded in 2013–14 (1.5 ± 0.4), and the lowest diversity was seen in 2008–09 (0.9 ± 0.5) (Figure 4a), with significant differences between them (p -value = 0.04).

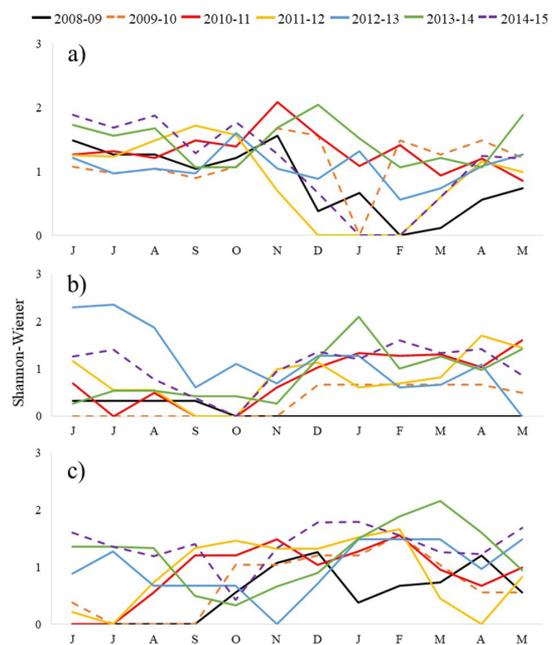


Figure 4. Reproductive phenological diversity of three species of *Miconia* growing in a tropical forest on the Lençóis River, Chapada Diamantina, northeastern Brazil. (a) *Miconia alborufescens*; (b) *M. holosericea*; and (c) *M. prasina*. The letters on the horizontal axis correspond to the months in each year of study.

3.2. Pattern, seasonality, and diversity of the reproductive phenology of *M. holosericea*

Miconia holosericea showed an annual, intermediate, and regular flowering pattern, with production peaks of floral buds (80% Fournier) and flowers (100% Fournier) in November and December, respectively, at the beginning

Table 1. Results of circular analysis for seasonal patterns of reproductive phenophases of *Miconia alborufescens* between June/2008 and May/2015 in a gallery forest on the Lençóis River, Chapada Diamantina, northeastern Brazil.

Years	Metrics	Bud	Flower	Immature Fruit	Mature Fruit
2008-09	Mean angle (μ)	186.37 ^o	210 ^o	330 ^o	0 ^o
	Mean date	Jul-06-2008	Jul-30-2008	Nov-29-2008	Jan-01-2009
	Variance	0.70	0.5	0.06	0
	r-value	0.3	0.5	0.9	1
	Rayleigh test (<i>p</i>)	0.003*	0.67	0.0*	0.03*
2009-10	Mean angle (μ)	111.79 ^o	289.37 ^o	308.17 ^o	343.90 ^o
	Mean date	Apr-22-2010	Oct-19-2009	Nov-07-2009	Dec-13-2009
	Variance	0.92	0.23	0.44	0.50
	r-value	0.08	0.8	0.6	0.52
	Rayleigh test (<i>p</i>)	0.6	0*	0.0002*	0.2
2010-11	Mean angle (μ)	183.43 ^o	272.49 ^o	292.60 ^o	309.90 ^o
	Mean date	Jul-03-2010	Oct-02-2010	Oct-22-2010	Nov-09-2010
	Variance	0.90	0.23	0.16	0.03
	r-value	0.99	0.8	0.8	0.96
	Rayleigh test (<i>p</i>)	0.4	0*	0*	0*
2011-12	Mean angle (μ)	315 ^o	330 ^o	67.24 ^o	122.31 ^o
	Mean date	Nov-14-2011	Nov-29-2011	Mar-08-2012	May-03-2012
	Variance	0.59	0.69	0.93	0.53
	r-value	0.4	0.3	0.07	0.47
	Rayleigh test (<i>p</i>)	0.0001*	0.02*	0.4	0
2012-13	Mean angle (μ)	138.43 ^o	293.79 ^o	285 ^o	306.88 ^o
	Mean date	May-19-2013	Oct-23-2012	Oct-14-2012	Nov-16-2012
	Variance	0.89	0.07	0.03	0.46
	r-value	0.1	0.9	0.96	0.54
	Rayleigh test (<i>p</i>)	0.45	0*	0*	0.005*
2013-14	Mean angle (μ)	185.75 ^o	161.93 ^o	35.10 ^o	116.41 ^o
	Mean date	Jul-06-2013	Jun-12-2013	Feb-04-2014	Apr-27-2014
	Variance	0.96	0.33	0.44	0.82
	r-value	0.04	0.97	0.56	0.2
	Rayleigh test (<i>p</i>)	0.9	0*	0.03*	0.4
2014-15	Mean angle (μ)	34.40 ^o	340.89 ^o	123.88 ^o	137 ^o
	Mean date	Feb-03-2015	Dec-10-2014	May-04-2015	May-17-2015
	Variance	0.56	0.12	0.27	0.11
	r-value	0.4	0.9	0.7	0.9
	Rayleigh test (<i>p</i>)	0*	0.9	0*	0*

*Significant results ($P < 0.05$).

of the rainy season (Figure 3b). Fruiting had an annual, intermediate to long, and regular pattern, with greater intensity of immature fruits (100% Fournier) from January to June, and of mature fruits (50% Fournier) from May to August (Figure 3b), corresponding to the wet-dry season transition. All of the phenophases were seasonal and

synchronous (except 2012–2013), with *r* vector values above 0.8 for flowering and 0.5 for fruiting; the mean dates of flowering occurred between September and February, while fruiting varied between January and July (Table 2).

Miconia holosericea showed interannual variations in its phenological patterns, which also coincided with the

Table 2. Results of circular analysis for seasonal patterns of reproductive phenophases of *Miconia holosericea* between June/2008 and May/2015 in a gallery forest on the Lençóis River, Chapada Diamantina, northeastern Brazil.

Years	Metrics	Bud	Flower	Immature Fruit	Mature Fruit
2008-09	Mean angle (μ)	330 ^o	330 ^o	63.87 ^o	195 ^o
	Mean date	Nov-29-2008	Nov-29-2008	Mar-04-2009	Jul-15-2008
	Variance	0	0	0.35	0.16
	r-value	1	1	0.65	0.84
	Rayleigh test (<i>p</i>)	0*	0*	0*	0.05*
2009-10	Mean angle (μ)	330 ^o	330 ^o	149.30 ^o	180 ^o
	Mean date	Nov-29-2009	Nov-29-2009	May-30-2010	Jun-30-2009
	Variance	0	0	0.54	0.09
	r-value	1	1	0.5	0.9
	Rayleigh test (<i>p</i>)	0.007*	0.007*	0*	0*
2010-11	Mean angle (μ)	315.80 ^o	333.13 ^o	97.54 ^o	151.61 ^o
	Mean date	Nov-15-2010	Dec-02-2010	Apr-07-2011	Jun-01-2010
	Variance	0.13	0.16	0.65	0.26
	r-value	0.9	0.8	0.3	0.7
	Rayleigh test (<i>p</i>)	0*	0.0001*	0*	0*
2011-12	Mean angle (μ)	315 ^o	330 ^o	67.24 ^o	122.31 ^o
	Mean date	Nov-14-2011	Nov-29-2011	Mar-08-2012	May-03-2012
	Variance	0.03	0	0.5	0.09
	r-value	0.97	1	0.5	0.9
	Rayleigh test (<i>p</i>)	0*	0*	0*	0*
2012-13	Mean angle (μ)	242.28 ^o	330 ^o	67.35 ^o	158.13 ^o
	Mean date	Sep-01-2012	Nov-29-2012	Mar-08-2013	Jun-08-2012
	Variance	0.82	0.78	0.91	0.5
	r-value	0.2	0.2	0.08	0.49
	Rayleigh test (<i>p</i>)	0.3	0.2	0.5	0*
2013-14	Mean angle (μ)	185.75 ^o	7.10 ^{-16o}	0.7 ^o	0.02 ^o
	Mean date	Dec-06-2013	Jan-01-2014	Jan-01-/2014	Jan-01-2014
	Variance	0.13	0.17	0.39	0.48
	r-value	0.9	0.8	0.6	0.52
	Rayleigh test (<i>p</i>)	0*	0*	0*	0.2
2014-15	Mean angle (μ)	309.14 ^o	60 ^o	76.68 ^o	139.60 ^o
	Mean date	Nov-08-2014	Feb-29-2015	Mar-17-2015	Mar-20-2015
	Variance	0.17	0	0.69	0.30
	r-value	0.8	1	0.3	0.7
	Rayleigh test (<i>p</i>)	0*	0.51	0.0001*	0*

*Significant results ($P < 0.05$).

occurrence of ENSO events, such as immature fruits in 2010–11 (La Niña) and 2014–15 (El Niño), and mature fruits during 2012–13 as compared to 2008–09 (La Niña) and 2013–14 (Table S3, Supplementary Material). The reproductive phenological diversity of *M. holosericea* was low (0.7 ± 0.6) during the study period. There was a decrease in diversity

in September (0.3 ± 0.4) and October (0.2 ± 0.4) during the dry-raining season and an increase in diversity in January (1 ± 0.7) during the rainy season. The highest diversity was recorded in 2012–13 (1.2 ± 0.7), and the lowest diversity was seen in 2008–09 (0.1 ± 0.2) (Figure 4b), with significant differences between them (p -value = $5.6 \cdot 10^{-5}$).

3.3. Pattern, seasonality, and diversity of the reproductive phenology of *M. prasina*

Miconia prasina exhibited an annual, intermediate, and regular flowering pattern, usually from September to December (Figure 3c). The phenophases of floral buds and flowers exhibited intensity peaks above 50% Fournier between October and November (beginning of the rainy season) until 2012 (Figure 3c), when a prolonged drought was recorded in the Chapada Diamantina region. In the following years, we observed a reduction in flowering intensity, with intensity peaks below 30%. Fruiting had an annual, intermediate to long, and regular pattern, with

greater production of immature fruits (60% Fournier) from December to January, and of mature fruits (30% Fournier) from February to March during the rainy season (Figure 3c). The reproductive phenophases were seasonal and synchronous, with r vector values above 0.5 for both flowering and fruiting, except 2013–14 and 2014–2015. The mean dates of flowering occurred from September to November, and mature fruits from December to April (Table 3), except 2013–14 and 2014–2015.

Interannual variations were detected only in relation to fruiting intensity in *M. prasina* (Table S4, Supplementary Material). Immature fruits varied in 2009–10 (El Niño),

Table 3. Results of circular analysis for seasonal patterns of reproductive phenophases of *Miconia prasina* between June/2008 and May/2015 in a gallery forest on the Lençóis River, Chapada Diamantina, northeastern Brazil.

Years	Metrics	Bud	Flower	Immature Fruit	Mature Fruit
2008-09	Mean angle (μ)	320.8 ^o	330 ^o	49 ^o	74 ^o
	Mean date	Nov-20-2008	Nov-29-2008	Feb-18-2009	Mar-15-2009
	Variance	0.32	0	0.33	0.34
	r-value	0.6	1	0.7	0.97
	Rayleigh test (p)	0.0004*	0*	0*	0*
2009-10	Mean angle (μ)	290.75 ^o	300 ^o	21.78 ^o	45 ^o
	Mean date	Oct-20-2009	Oct-30-2009	Jan-22-2010	Feb-14-2010
	Variance	0.22	0	0.31	0.03
	r-value	0.8	1	0.7	0.96
	Rayleigh test (p)	0*	0*	0*	0*
2010-11	Mean angle (μ)	263.93 ^o	271.77 ^o	353.79 ^o	54.48 ^o
	Mean date	Sep-23-2010	Oct-01-2010	Dec-23-2010	Feb-24-2011
	Variance	0.25	0.38	0.52	0.08
	r-value	0.8	0.6	0.5	0.9
	Rayleigh test (p)	0*	0.003*	0*	0*
2011-12	Mean angle (μ)	259.16 ^o	286.12 ^o	339.85 ^o	24.36 ^o
	Mean date	Sep-18-2011	Jun-30-2011	Jun-17-2011	Jan-24-2012
	Variance	0.45	0.17	0.31	0.21
	r-value	0.54	0.8	0.7	0.97
	Rayleigh test (p)	0*	0*	0*	0*
2012-13	Mean angle (μ)	163 ^o	180 ^o	63.07 ^o	42.41 ^o
	Mean date	Jun-13-2012	Jun-30-2012	Mar-03-2013	Feb-12-2013
	Variance	0.31	0	0.53	0.32
	r-value	0.7	1	0.46	0.7
	Rayleigh test (p)	0.001*	0.03*	0.0004*	0*
2013-14	Mean angle (μ)	316.60 ^o	330 ^o	83.08 ^o	106.81 ^o
	Mean date	Nov-16-2013	Nov-29-2013	Mar-24-2014	Apr-17-2014
	Variance	0.61	0.25	0.66	0.66
	r-value	0.4	0.8	0.3	0.4
	Rayleigh test (p)	0.1	0.006*	0.001*	0.002*
2014-15	Mean angle (μ)	236.61 ^o	135.30 ^o	3.59 ^o	23.59 ^o
	Mean date	Aug-26-2014	May-16-2015	Jan-03-2015	Jan-23-2015
	Variance	0.62	0.10	0.57	0.45
	r-value	0.4	0.9	0.4	0.55
	Rayleigh test (p)	0.0007*	0*	0*	0*

*Significant results ($P < 0.05$).

with lower yields than 2010–11 (La Niña) and 2014–15 (El Niño), and 2012–13 compared to 2013–14. Mature fruits varied between the El Niño event of 2009–10, with lower annual productions than 2012–13, 2013–14, and 2014–15. Significant differences were also observed between 2011–12 compared to 2012–13 and 2014–15. The Friedman test showed that there were no variations in flowering (Table S4, Supplementary Material). The reproductive phenological diversity of *M. prasina* (Figure 4c) presented a total mean of 0.9 ± 0.6 for the study period. There was a decrease in diversity in July (0.6 ± 0.7) at the beginning of the dry season, and a diversity peak in February (1.5 ± 0.4) during the rainy season (see Figures S1 and S2, Supplementary Material). The year 2008–09 showed the lowest mean diversity value (0.5 ± 0.5), and 2014–15 (1.4 ± 0.4) the highest mean value (Figure 4c), with significant differences between them (p -value = 0.002).

4. Discussion

Based on a seven-year series, we observed predominantly annual, seasonal, and synchronous patterns of flowering and fruiting in three sympatric species of *Miconia* growing in a gallery forest in the Chapada Diamantina mountains, with intraspecific synchrony and little interspecific overlap, confirming our initial hypothesis. Flowering was concentrated during the dry-rainy season transition, and fruiting occurred mainly during the rainy season. The seasonal rhythms evidenced interannual variations in terms of the mean dates of reproductive phenophases coinciding with ENSO events, as expected. Intrapopulational reproductive phenological diversity was high, tending to increase (i.e., less synchrony) in ENSO years, as in *M. prasina* (2014–15), and prolonged drought events. Our findings contrast with those of Brito et al. (2017) who identified aseasonality and high interspecific synchrony/overlap at the family level in terms of both flower and fruit production of Melastomataceae in the Atlantic Forest. Those results appear to reflect phenological patterns associated with distinct reproduction and dispersal systems. Those authors, however, noted that pollinator-dependent species evidenced seasonality even in rainforest. This was the case of the pollinator-dependent *Miconia* species evaluated here, with their reproductive phenophases being mostly seasonal, thus corroborating, in this respect, the findings of Brito et al. (2017) as well as others studies (Pereira et al., 2024). The relationship between the seasonality of flowering of melittophilous species and the greater abundance and richness of bees in warmer seasons has been suggested in other studies (Hoiss et al., 2012). The seasonal flowering of pollinator-dependent species of Melastomataceae therefore reinforces this trend.

The intraspecific synchrony observed among the plants studied here may be linked to their potentiation for attracting pollinators, as massive flowering can increase the frequency of visits and dilute damage caused by herbivores due to the greater number of individuals in their reproductive stage (van Schaik et al., 1993). The sequential pattern of production of interspecific flowers, with low overlap, may also be a consequence of

selective pressures exerted by competition for pollinators (Gentry, 1974; Brito et al., 2017). The poricidal anthers of Melastomataceae flowers restrict their pollination to vibrating bees (98% of pollinators) (Dellinger et al., 2022) so that the temporal distribution of flowering among the *Miconia* species studied here would reduce competition for pollinators. Additionally, as indicated by Vilela et al. (2014), the sequential flowering of sympatric species of the same family already helps to sustain pollinators.

The fruiting of *Miconia* species occurring mainly in the rainy season, with high intraspecific synchrony and little apparent interspecific overlap, demonstrates temporal segregation in the supply of bacoid fruits (which are basically composed of water and sugars) which are important resources for frugivores in tropical forests (Brito et al., 2017). Several other studies have reported segregated fruiting patterns of fleshy-fruited species of Melastomataceae, mainly those belonging to the Miconieae tribe, in low, seasonal forests, as listed by Brito et al. (2017). The seasonality of fruiting of sympatric species of *Miconia* reinforces the view that both the formation and attractiveness of these types of fruits are favored by the availability of plentiful water supplies (Brito et al., 2017; Moungrsrimuangdee et al., 2017; Sierra and Blanco, 2021). Furthermore, the production of mature fruits during the rainy season, as seen with *M. alborufescens* and *M. prasina*, is considered crucial for seed germination and seedling establishment (Moungrsrimuangdee et al., 2017). The intensity and periodicity of the phenologies of tropical forest plants can vary during different years as a function of global climatic phenomena such as El Niño and La Niña (Chang-Yang et al., 2016; Menezes et al., 2017; Chapman et al., 2018; Gateau-Rey et al., 2018). Our results indicate that flowering was the phenophase with the lowest variation of annual productivity in two thirds of the *Miconia* species studied (Tables S2, S3, and S4, Supplementary Materials), and therefore maintained the resources consumed by buzz-pollination bees (Barônio et al., 2016; Sierra and Blanco, 2021; Dellinger et al., 2022).

ENSO events are classified according to their intensity as weak, moderate, or strong (Souza and Reboita, 2021), and they may affect the reproductive phenology of the studied *Miconia* species with different intensities, as was seen, for example, in the strong El Niño of 2014–15 when higher fruit productivity of *M. holosericea* was observed (statistically different from the 2009–10 results, when a moderate El Niño occurred). La Niña years were marked by intense precipitation and low averages temperatures, photoperiods, and insolation. These climate changes caused by different intensities of La Niña can also affected plant reproductive phenophases (Moungrsrimuangdee et al., 2017), as was observed here in the periods 2010–11 (strong) and 2011–12 (moderate), with increases in immature fruits productivity by both *M. holosericea* and *M. prasina* as compared to El Niño events (2014–15 and 2009–10, respectively).

Miconia holosericea produced less immature and mature fruits during the 2014–15 El Niño event. Gateau-Rey et al. (2018) reported similar results when analyzing cocoa forests in southern Bahia State, Brazil (with decrease in fruit production of up to 89%). On the other hand,

M. prasina fruited with greater intensity during the occurrence of La Niña and El Niño events (as in 2008–09, 2010–11, 2011–12 and 2014–15), apparently favored by climatic conditions positively related to its reproductive phenology. Chapman et al. (2018) also reported increased fruiting associated with ENSO events when they evaluated a 15-year phenological dataset of tropical rainforest tree species in Uganda. This same pattern of increased intensity of reproductive phenology following ENSO events was also seen with lianas in Australian tropical forests based on the analysis of a 15-year phenological dataset (Vogado et al., 2022). Such changes in reproductive phenological patterns related to ENSO events suggest a possible increase in the abundance of these species in tropical forests as result of climate change, thus contributing to alterations in the composition and structure of their respective phytophysiognomies (Vogado et al., 2022).

Although there were no ENSO events in 2012, the Chapada Diamantina region suffered the effects of a prolonged drought, which negatively impacted the fruiting intensity of *M. prasina*, and synchrony of fruiting of *M. alborufescens* and *M. holosericea*; *M. prasina*, however, remained synchronous. Those variations may have been influenced by intense fruiting in the previous year (Williams-Linera and Meave, 2002). The fruiting pattern may also have been influenced by low water availability, which limited the production of fleshy fruits (Brito et al., 2017).

Our study is the first to use diversity indices to assess variations in long time series of phenological data. The phenological diversity of the *Miconia* species studied here appears to reflect the synchrony and seasonality of their phenophases. *Miconia alborufescens* showed the highest phenological diversity among the three sympatric species, converging with its continuous reproductive phenological pattern. The lower diversity observed in *M. holosericea*, must be related to its high synchrony and marked seasonality, with more well-defined flowering and fruiting intervals than seen in other *Miconia* species (Goulart et al., 2005; Costa et al., 2021). The peaks and troughs of phenological diversity among the species studied demonstrated their phenological rhythms (Goulart et al., 2005; Costa et al., 2021), and the temporal segregation of flowering and fruit production should favor pollination and dispersion strategies (Souza and Funch, 2017; Pereira et al., 2024). The period of greater activity coincides with the periods of lesser activity of the other two species with, for example, the progressive increase of phenological diversity of *M. holosericea* in January, of *M. prasina* in February, with a decrease in the phenological diversity of *M. alborufescens*. This dynamic tends to minimize competition for shared pollinators and dispersers (Neves et al., 2010; Barônio et al., 2016).

The species of *Miconia* studied here showed reproductive phenological patterns that were mostly annual and seasonal, with sequential rhythms, starting with *M. alborufescens*, followed by *M. holosericea*, and then *M. prasina*, thus minimizing the overlapping of their flowering and fruiting cycles. The global phenomena of El Niño and La Niña influenced the climatic conditions of the study area and affected the production of flowers and

fruits of the sympatric *Miconia* species. Periods of El Niño can cause variations in the phenological diversity in the *Miconia* species studied, with consequent impacts on their phenologies. The strong El Niño of 2014–15 coincided with the high phenological diversity in *Miconia prasina*, altering its phenological synchrony (Santos et al., 2020; Costa et al., 2021). The La Niña event occurred in 2008–09 caused low diversity in *Miconia* species, with the distribution of rainfall in the 2008–09, 2010–11, and 2011–12 periods apparently favoring high flower and fruit production. This work emphasizes the utility of the diversity index as a tool for comprehending the interannual variability of phenological responses in the context of changing climatic conditions associated with ENSO.

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Supplementary Material

Supplementary material accompanies this paper.

Figure S1. Annual reproductive phenological diversity of three *Miconia* species in a tropical forest in the Chapada Diamantina mountains. (a) *M. alborufescens*, (b) *M. holosericea*, and (c) *M. prasina*. Different letters represent significant statistical differences (ANOVA, $P < 0.05$).

Figure S2. Monthly means of reproductive phenological diversity for three *Miconia* species in a tropical forest in the Chapada Diamantina mountains range between 2008-2015.

Table S1. Listings of El Niño and La Niña events in the period 2008-2015 as defined by SSTs in the Niño 3.4 region, based on the $\pm 0.5^{\circ}\text{C}$ limit for the ONI index. The starting and ending month of each is given along with the duration in months.

Table S2. Results of the Fridman and Wilcoxon tests applied to the reproductive phenophases (intensity) of *Miconia alborufescens* between June/2008 and June/2015.

Table S3. Results of the Fridman and Wilcoxon tests applied to the reproductive phenophases (intensity) of *Miconia holosericea* between June/2008 and June/2015.

Table S4. Results of the Fridman and Wilcoxon tests applied to the reproductive phenophases (intensity) of *Miconia prasina* between June/2008 and June/2015.

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