

Phenology of Critically Endangered Myrcia ovina in Sergipe

PHENOLOGY OF A CRITICALLY ENDANGERED MYRTACEAE SPECIES

IN A RESTINGA AREA IN NORTHEASTERN BRAZIL: *MYRCIA OVINA*

PROENÇA & LANDIM

Amadeu dos Santos-Neto^{1*} , *Eduardo Vinícius da Silva Oliveira*²  & *Myrna Friederichs*

*Landim*³ 

¹ South Dakota State University, Department of Biology and Microbiology, 1224 Medary Ave., Brookings, SD 57007, United States of America

² Universidade Federal de Sergipe, Programa de Pós-Graduação em Ecologia e Conservação, Av. Marechal Rondon, s/n, Jd. Rosa Elze, CEP 49100-000, São Cristóvão, SE, Brasil

³ Universidade Federal de Sergipe, Departamento de Biologia, Av. Marechal Rondon, s/n, Jd. Rosa Elze, CEP 49100-000, São Cristóvão, SE, Brasil

E-mails: amsneco@gmail.com (*corresponding author); eduardovso@yahoo.com.br; m_landim@hotmail.com

Abstract. Restinga ecosystems in Brazil are characterized by harsh environmental conditions and high biodiversity, yet many of their endemic plant species remain poorly studied. Understanding the reproductive ecology of these species is essential for developing effective conservation strategies. This study investigated the ecological and reproductive strategies of *Myrcia ovina*, an endemic and critically endangered shrub in Restinga. We monitored phenological events over a 12-month period and analyzed vegetative and reproductive patterns with circular statistics and correlations with climatic variables (temperature and precipitation). Observations also included vegetative behavior and potential ecological drivers of reproductive timing. Our findings indicate that *Myrcia ovina* is an evergreen species with continuous leaf exchange, which is an important trait for maintaining

photosynthesis in nutrient-poor soils. The species exhibits a marked annual flowering peak during the dry season, likely aligning with pollinator availability and reducing herbivory pressure. Fruit development peaks at the beginning of the rainy season, when increased water availability may support seed maturation. However, seed dispersal may be less effective during this period due to reduced frugivore activity in the presence of more abundant food sources. The positive correlation between bud production and preceding precipitation highlights the role of historical moisture availability in reproductive success. These results demonstrate how *Myrcia ovina* is finely tuned to the seasonal dynamics of the Restinga and offer important insights into the adaptive strategies of Myrtaceae species in tropical coastal systems. This study contributes valuable knowledge for biodiversity conservation in these vulnerable ecosystems.

Keywords: Coastal Plain; Plant Reproduction; Tropical Ecosystems; Vegetation Dynamics

INTRODUCTION

Phenology encompasses the study of the timing of biological events in organisms, such as growth, development, reproduction, and other seasonal behaviors, over time. Phenological investigations of species and/or plant assemblages contribute to generating information on aspects related to their reproduction (Talora & Morellato 2000), vegetation regeneration (Sakai & Kitajima 2019), and the temporality of resource distribution for fauna (Elhalawany & Abou-Setta 2013), which are essential not only for understanding ecosystem dynamics but also for guiding environmental management strategies, such as fire regime planning, to support biodiversity and resource availability (Dos Santos Ferreira *et al.* 2023).

The phenological cycle of plant species is closely connected to climatic patterns (Marques *et al.* 2004) and appears to respond rapidly to the environmental changes observed in recent decades (Menzel *et al.* 2020). Thus, interest in studying these patterns has increased in recent years due to the use of phenology as a tool to assess and address the environmental impacts caused by global climate

change (Park *et al.* 2023). However, the relationships between phenophases and climatic variables are not uniform across biomes. In temperate regions, phenological events such as leaf-out, flowering, and fruiting are often tightly linked to temperature and photoperiod, whereas in tropical regions, these events are more commonly influenced by rainfall patterns and inter-annual climatic variability (Wright & Calderón 2006, Chapman *et al.* 2018). Additionally, phenological strategies vary among plants with different habits and life forms—for instance, herbaceous species, lianas, and canopy trees may exhibit distinct phenological responses even within the same environment (Borchert *et al.* 2005). Moreover, phylogenetic history can shape phenological behavior, as closely related species often share similar responses to environmental cues, reflecting evolutionary constraints and adaptations (Davies *et al.* 2013). Understanding these diverse phenological strategies is essential for predicting ecosystem responses to climate change across different ecological and evolutionary contexts.

Plant communities in tropical and subtropical ecosystems tend to exhibit highly diverse (Sakai & Kitajima 2019) and complex (Newstrom *et al.* 1994) phenological patterns. Although knowledge about the phenology of tropical plant communities has increased in recent years (Ssali & Sheil 2023, Bezerra-Silva *et al.* 2024), much progress has been driven by the adoption of new technologies and data collection methods, such as special cameras, satellite imagery, and more advanced software (Gray & Ewers 2021). Despite these advances, many gaps in our understanding remain (Davis *et al.* 2022a). Importantly, these technological developments have enabled more continuous, large-scale, and high-resolution monitoring of phenological events, allowing researchers to detect subtle changes in timing and patterns that were previously unobservable (Gong *et al.* 2024). This has improved predictions of ecosystem responses to climate change and facilitated better conservation strategies in tropical regions (Gao & Zhang 2021).

Phenological studies in tropical ecosystems face challenges due to high biodiversity, complex structures, and remote locations. These factors complicate species monitoring, while microclimatic variations demand detailed spatial and temporal data (Blonder *et al.* 2018). Additionally, long-term

research on climate change responses requires sustained funding, making these studies more difficult than those in temperate regions, where research dates back to the 17th century (Abernethy *et al.* 2018). Among these tropical ecosystems are the Restingas, floristically complex ecosystems established on Brazil's coastal plain. They have historically been among the most degraded in the country and are still under intense human pressure.

In these environments, Myrtaceae stands out for its richness, abundance, and ecological importance (Melo *et al.* 2023). This family, which includes genera such as *Psidium*, *Eugenia*, and *Myrcia*, is often dominant in Restinga forests and plays a central role in structuring plant communities. Myrtaceae species provide year-round resources such as nectar, pollen, and fleshy fruits, making them vital to a wide array of frugivores and pollinators. They are particularly important for pollinator species and dispersers, notably birds (Caselli & Setz 2011) and primates (Canale *et al.* 2016), and contribute to ecosystem connectivity and regeneration.

In Northeastern Brazil, the Restinga ecosystems of the state of Sergipe have been extensively studied over the past decade, with advances in knowledge of their plant (E. V. S. Oliveira & Landim 2014, dos Santos-Neto *et al.* 2024) and animal communities (Bezerra & Bocchiglieri 2021). However, the lack of knowledge about the phenological patterns of Restingas in Sergipe is still pronounced (dos Santos-Neto *et al.* 2018). In this context, given the scarcity of studies and the need to expand knowledge about the phenology of Restinga species, this study aims to describe the phenological cycle of a Myrtaceae species with a restricted spatial distribution, apparently limited to the northern coast of Sergipe, *Myrcia ovina* Proença & Landim, and to assess how the species' phenology is related to environmental factors. We hypothesize that *Myrcia ovina* has seasonal reproductive phenology associated with climatic variables such as rainfall and temperature, particularly flowering during the dry season and fruiting at the onset of the rainy season, as observed in other Myrtaceae species in coastal ecosystems (Bencke & Morellato 2002, Marques & Oliveira 2004a).

MATERIAL AND METHODS

Study Area

This study was conducted in the Restinga area of Lagoa Redonda village, Pirambu, on Sergipe's northern coast (Figure 1). The regional climate is tropical with a dry summer (As) *sensu* Köppen-Geiger classification (Alvares *et al.* 2013), with an average annual temperature of 25.5°C and 1,073 mm of annual precipitation (Souza *et al.* 2001). The rainy season lasts from March to August, and the dry season lasts from September to February (Oliveira *et al.* 2015). The area lies within the Coastal Plain and Coastal Plateaus, featuring podzolic soils and part of the Atlantic East Watershed and Japaratuba River Basin.

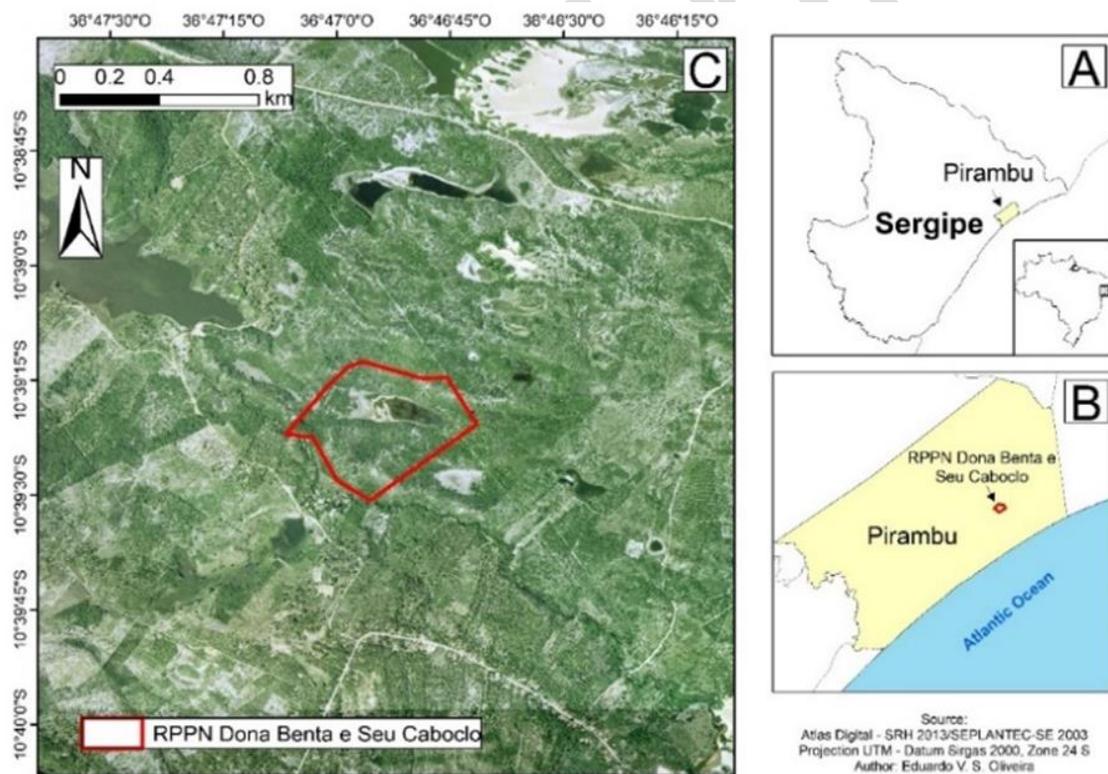


Figure 1. Location of Dona Benta e Seu Caboclo Private Natural Heritage Reserve (RPPN) on the northern coast of the state of Sergipe, Brazil.

Data collection was carried out at the Private Natural Heritage Reserve (RPPN) *Dona Benta e Seu Caboclo* (Figure 2). This protected area, a sustainable use conservation unit under the National System of Conservation Units (Law No. 9.985 of 18 July 2000), was established by ordinance No. 71 on August 27, 2010, by the Chico Mendes Institute for Biodiversity Conservation (ICMBio). It covers 23.6 hectares within the Cordeiro de Jesus Farm (97.1 hectares) and is a poorly known protected area.



Figure 2. Environments of the *Dona Benta e Seu Caboclo* Private Natural Heritage Reserve, state of Sergipe, Brazil. a – shrub vegetation on sandy soils, b – open shrubland, c – temporary freshwater lagoon, d – dune formation with surrounding vegetation. Author: Amadeu M. Santos-Neto

Studied Species

Myrcia ovina (Figure 3), a shrub of the Myrtaceae family (Proenca *et al.* 2014), has berry-type fruit with zoochoric dispersal (Oliveira & Landim 2020). It typically grows 1–2 meters tall and occurs in the Atlantic Forest domain and in rocky outcrops of highland wetlands (Lima 2017, Alves *et al.*

2024). The species produces small, white flowers arranged in axillary inflorescences, which are likely pollinated by generalist bees, as commonly observed in other *Myrcia* species. Its fruits are fleshy, berry-type, and dark-colored when mature, suggesting adaptation for zoochoric dispersal, primarily by birds or small mammals. The seeds are small and likely dispersed through endozoochory. A distinctive feature is the dense covering of white trichomes across all plant organs, which is particularly prominent in younger individuals. Due to its restricted distribution and habitat encroachment, *Myrcia ovina* has a suggested classification of Critically Endangered (Lima 2017, IUCN 2018).



Figure 3. Details of the reproductive and vegetative features of *Myrcia ovina* Proença & Landim in the Restingas of the municipality of Pirambu, north coast of Sergipe, Brazil. a – floral buds, b – inflorescences at the beginning of anthesis, c – flowers in anthesis, d – branch with leaves and inflorescences. Author: Amadeu M. Santos-Neto.

Field Sampling

This study began in October 2017 with the selection and georeferencing of 23 individuals of *Myrcia ovina* Proença & Landim. Over the course of a year (ending in September 2018), data were collected monthly on six predefined phenophases: i. leaf emergence, ii. leaf shedding, iii. bud sprouting, iv. flowering, v. immature fruits, and vi. mature fruits (Bencke & Morellato 2002).

Two phenological assessment methods were used: (i) Fournier's Intensity Index – FI (Table 1), and (ii) the Phenological Activity Index – AI (Fournier 1974, Bencke & Morellato 2002). For each individual, six phenophases were recorded and the phenophases intensities were estimated visually. These observations formed the basis for both the FI and AI calculations. Observations were made in the field using binoculars when necessary, and each sampling session occurred within a consistent time window to minimize variation caused by daily or weather-related changes.

FI is considered the most suitable method for phenological studies involving one or a few species, as it provides more refined results, such as identifying peak periods of phenophase intensity within populations (San Martín-Gajardo & Morellato 2003). To avoid discrepancies, data collection was conducted by the same researcher throughout the study. The Activity Index (AI), which is based solely on the presence or absence of phenophases, provides an objective measure of a population's synchronization level (Bencke & Morellato 2002). To classify the flowering and fruiting frequency patterns of the *Myrcia ovina* population, the system of Newstrom et al. (1994) was used, which identifies four classes: "continuous", "sub-annual", "annual", and "supra-annual.". Abiotic variable data were obtained from three sources: (1) temperature (minimum, average, and maximum) data were sourced from the Northeast Real-Time Climate Monitoring Program (<http://proclima.cptec.inpe.br/>), which is managed by the Brazilian Superintendence for the Development of the Northeast and the Ministry of National Integration; (2) daily precipitation data for Pirambu were collected from the "Agritempo" platform (<https://www.agritempo.gov.br/agritempo/index.jsp>), which is maintained by the Brazilian Agricultural Research Corporation; and (3) photoperiod was calculated using the "Geosphere" package in R (Hijmans 2018).

Data Analysis

The flowering pattern was classified based on Gentry (1974), who identified four types for bee-pollinated plants: “steady-state”, “cornucopia”, “big-bang”, and “multiple-bang”. *Steady-state* species produce a few flowers daily over long periods. *Cornucopia* plants flower heavily for several weeks, attracting a wide range of bee species. *Big-bang* plants bloom all at once in a short period, depending on opportunistic pollinators. *Multiple bang* species flower in several brief, synchronized bursts throughout the year (Gentry 1974).

The Shapiro-Wilk test was used to assess the normality of the data distribution (San Martín-Gajardo & Morellato 2003). When detecting non-normality in the data, Spearman's rank correlation coefficient (ρ) was used. Data on the intensity of phenophases and the number of individuals showing the phenophases simultaneously were correlated with accumulated precipitation [i. the same month, ii. the previous month, iii. two months prior, iv. three months prior, v. four months prior, and vi. the historical average], as well as with minimum, maximum, and mean temperature, and day length.

As previously described, we employed two phenological indices, the Fournier Index and the Activity Index, to quantify the monthly phenological patterns for each phenophase. Because the two indices were highly correlated across all phenophases ($\rho = 0.67$ to 0.99), we selected the Activity Index for circular statistical analyses to avoid redundant transformation. For these analyses, individual observation dates (i.e., the dates on which phenophase activity was recorded) were converted into day-of-year values (1–365) and then into angles in degrees ($1 \text{ day} = 0.9836^\circ$) following Morellato *et al.* (2010). Circular statistics were applied separately for each phenophase and species, using the dates of observed activity (i.e., the presence of individuals showing the phenophase) as the circular data points. From these, we calculated the mean vector direction (μ), mean vector length (R), circular standard deviation, and the Rayleigh test statistic (z) and its associated p-value. Values of $R > 0.5$ indicate that observations are concentrated around a specific time of year (i.e., strong

seasonality), whereas $R < 0.5$ suggests greater temporal dispersion. All statistical analyses were conducted in R using the “Circular” package (R Development Core Team 2022; Lund et al. 2024).

RESULTS

Leaf Emergence and Leaf Shedding

The mean angle for leaf emergence was $333.476^\circ (\pm 120.865^\circ)$, 339th day of the year/ December 5th), with a mean vector r of 0.108. The average intensity was $20.58 (\pm 6.53)$, and the mean number of individuals exhibiting this phenophase monthly was $16 (\pm 4.22)$. This event was continuous ($Z = 2.242$, $p > 0.05$), with no clear intensity peak, and the lowest intensity was recorded in May (Figure 4).

Ahead of print

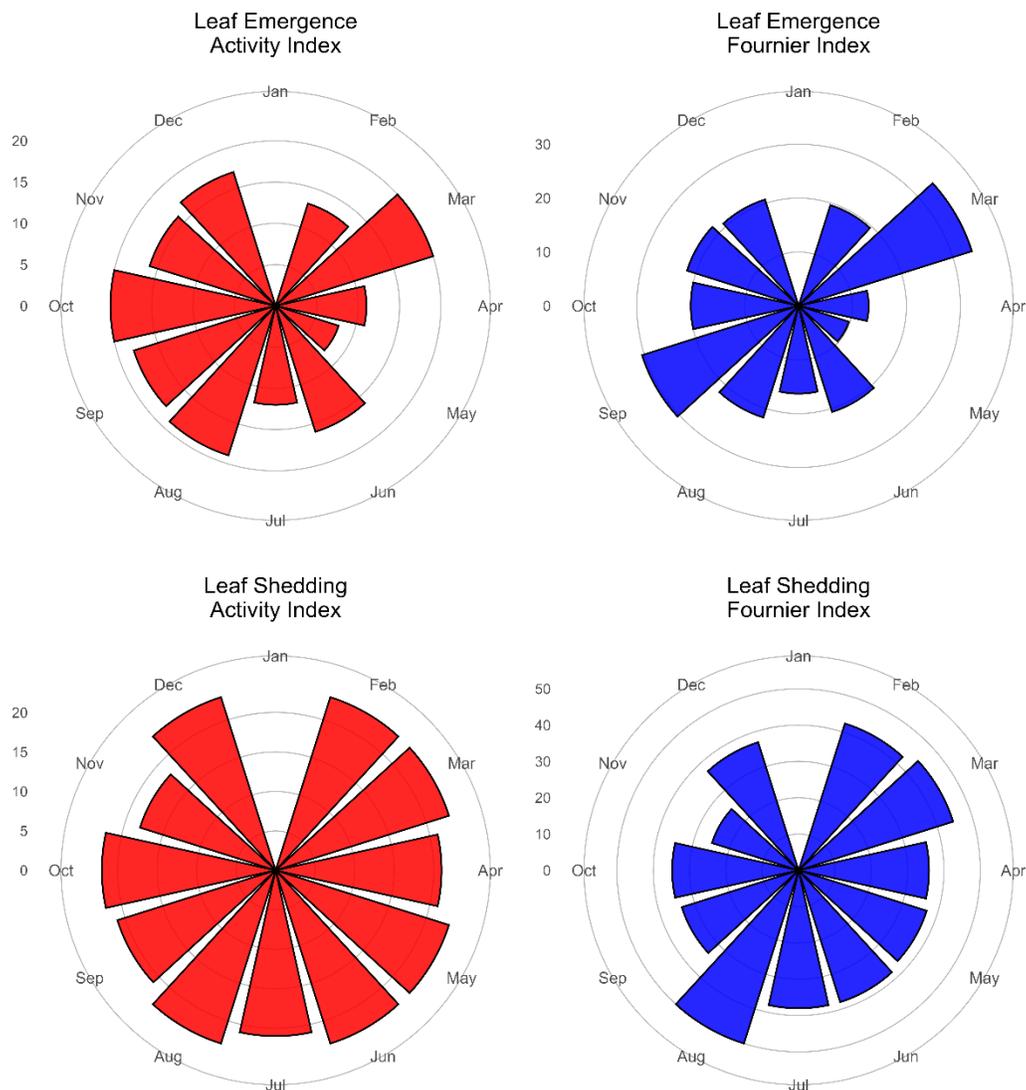


Figure 4. Phenophases of Leaf Growth and Defoliation of the species *Myrcia ovina* along the year, based on two phenological indices, the “Activity Index” and the “Fournier Intensity Index” at Dona Benta e Seu Caboclo Private Natural Heritage Reserve, state of Sergipe, Brazil.

The mean angle for leaf shedding was 109.484° ($\pm 158.616^{\circ}$, 111th day of the year, April 21st), with a mean vector r of 0.022. Like leaf emergence, leaf shedding was also continuous ($Z = 0.123$, $p > 0.05$). The peak in leaf shedding was observed in August, and the lowest intensity was recorded in November (Figure 4). On average, the intensity of this phenophase was 38 (± 6.12), with approximately 22 (± 1.50) individuals observed showing this phenophase monthly.

Bud Sprouting and Flowering

The mean angle for flower bud production was 337.721° ($\pm 47.448^\circ$, 343rd day of the year/ December 9th), with a mean vector r of 0.71. This event spanned six months, starting in August and ending in January, with its peak in November (Figure 5). Flower buds were also observed in April and June, but only in a single individual at low intensity. This phenophase was seasonal ($Z = 35.258$, $p < 0.001$). The flowering of the studied population of *Myrcia ovina* can be classified as 'cornucopia', with the production of a considerable number of flowers over more than eight weeks.

Ahead of print

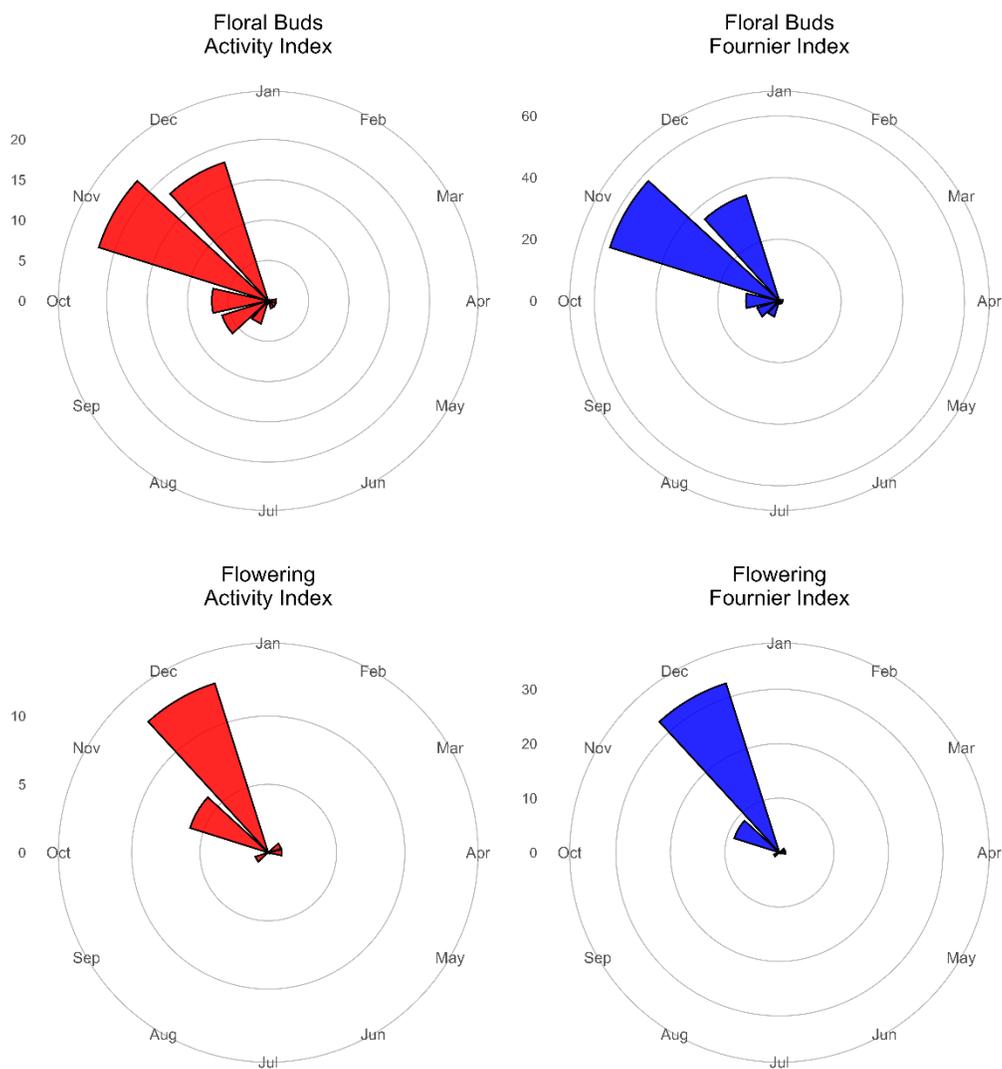


Figure 5. Phenophases of Buds sprouting and Flowering species *Myrcia ovina* along the year, based on two phenological indices, the “Activity Index” and the “Fournier Intensity Index” at Dona Benta e Seu Caboclo Private Natural Heritage Reserve, state of Sergipe, Brazil.

Flowering was a seasonal event ($Z = 22.725$, $p < 0.001$). The mean angle for flowering was $7.181^\circ (\pm 34.994^\circ, 7\text{th day of the year/January 7th})$, with a mean vector r of 0.83. The flowering period lasted three months, starting in November, peaking in December, and ending in January (Figure 5). Like flower bud sprouting, flowers were also observed in other months throughout the year, but at low intensity.

Immature and Mature Fruits

The occurrence of immature fruits was also seasonal ($Z = 16.561$, $p < 0.001$). The mean angle for immature fruits was 31.799° ($\pm 27.922^\circ$, 32nd day of the year/February 1st), with a mean vector r of 0.888. These fruits were observed over a four-month period, starting in November and ending in February, peaking in January (Figure 6).

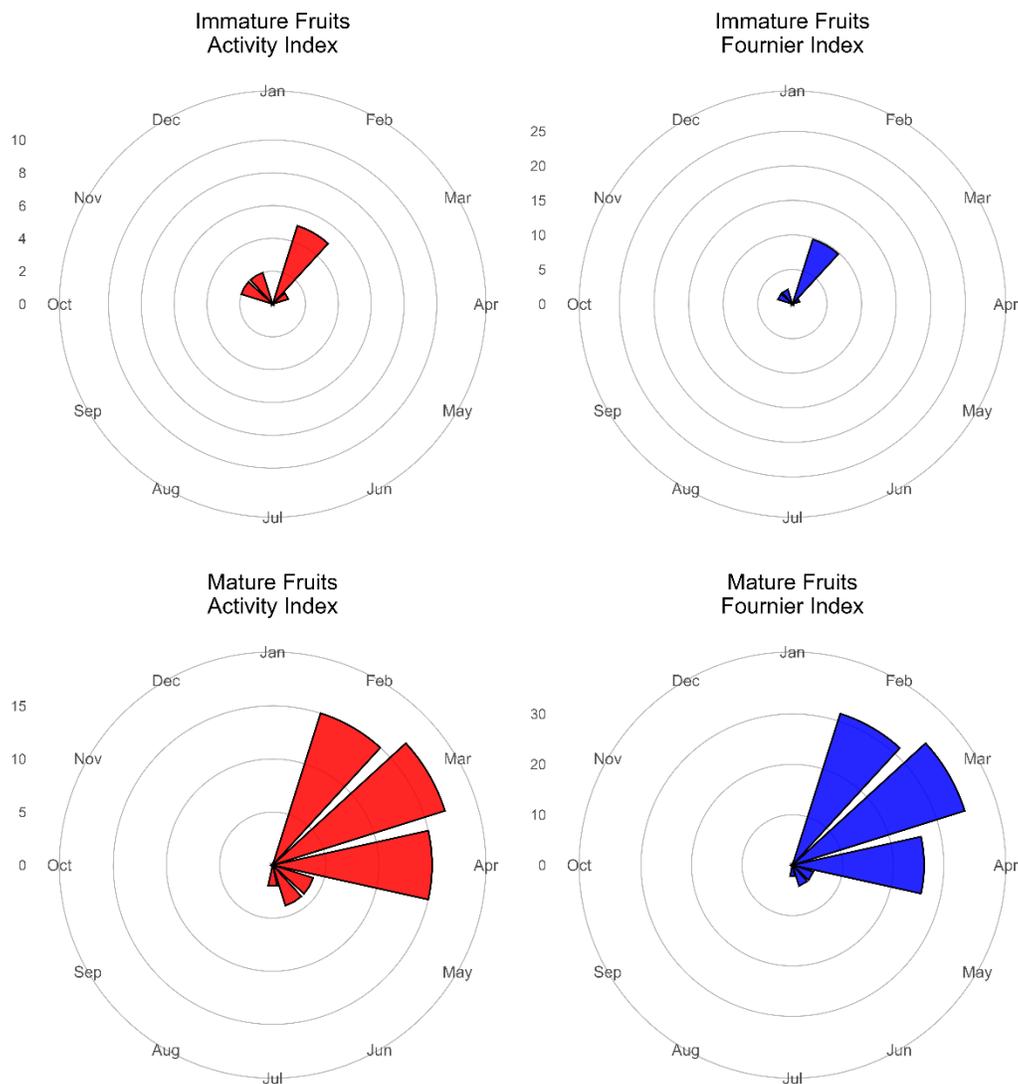


Figure 6. Phenophases of Immature Fruits and Mature Fruits of *Myrcia ovina* along the year, based on two phenological indices, the “Activity Index” and the “Fournier Intensity Index” at Dona Benta e Seu Caboclo Private Natural Heritage Reserve, state of Sergipe, Brazil.

The mature fruit phenophase also showed a seasonal pattern ($Z = 36.661$, $p < 0.001$). The mean angle for mature fruits was $87.371^\circ (\pm 45.563^\circ)$, 88th day of the year/March 29th), with a mean vector r of 0.729. Mature fruits were observed over a seven-month period, from January to June, with a peak in March (Figure 6).

Relationship of the phenophases with the Climate variables

No correlation was observed between leaf growth and the climatic variables analyzed: precipitation, day length and temperature (tMin, tAve and tMax) (Table 1). Bud sprouting was inversely correlated with the precipitation of the current month and positively correlated with prior precipitation with a time lag of three and four months (Table 1). The pattern of flower exposure was negatively correlated with the precipitation of the current month, the previous month, and the historical average, and positively correlated with day length and minimum, average, and maximum temperatures (Table 1).

Table 1 Results of the Spearman correlation between BS = "Buds Sprouting", FL = "Flowering", IF = "Immature Fruits", MF = "Mature Fruits", LE = "Leaf Emergence" and LF = "Leaf Shedding" with the environmental variables of precipitation: current, historical average, #1 (previous month), #2 (previous two months), #3 (previous three months), #4 (previous four months), temperature: tMin (minimum), tMean (average) and tMax (maximum) and photoperiod. "***" < 0.05 , "**" < 0.001 .

	Rainfall						Day length		Temperature	
	Current	Historical	#1	#2	#3	#4	DL	tMin	tAve	tMax
LE	-0.50	-0.5	-0.1	0.18	0.34	0.24	0.22	0.09	0.11	0.14
LS	0.12	0.02	-0.04	-0.45	-0.44	-0.30	-0.1	0.09	-0.06	-0.02
BS	-0.63*	0.00	-0.1	-0.6	0.76**	0.74**	0.51	0.11	0.32	0.32
FL	-0.71**	-0.70**	-0.63*	-0.2	0.18	0.36	0.70*	0.65*	0.69*	0.63*
IF	-0.57*	0.80**	-0.71*	-0.5	-0.10	0.31	0.82**	0.83**	0.86**	0.85**
MF	0.49	0.25	-0.20	-0.75**	-0.91**	-0.73**	-0.20	0.31	0.05	0.04

DISCUSSION

In general, *Myrcia ovina* can be considered an evergreen species, as it does not exhibit a period of intense (or complete) leaf shedding and leaf emergence can be observed throughout the year. This pattern has also been observed in other Myrtaceae species, such as *Myrcia insularis* Gardn, *Myrcia multiflora* (Berg) Legrand, and *Psidium cattleianum* Sabine in a Restinga in southern Brazil (Morellato *et al.* 1989). However, based on other studies in Brazilian Restingas, this does not appear to be the most common pattern observed in Myrtaceae species (Marchioretto *et al.* 2007). Species with continuous sprouting also seem to be rare (Machado 2018) in the Atlantic Forest of Sergipe, where the pattern of leaf emergence throughout the year has been detected in only a few species, such as *Tapirira guianensis* Aubl (Santos & Ferreira 2013). The continuous leaf shedding by Restinga plant species plays an important ecological role in maintaining soil fertility under the typically oligotrophic conditions of these ecosystems (Pires *et al.* 2006a, L. da S. Brito *et al.* 2018, Camara *et al.* 2018). Additionally, species established in Restingas are affected by nutrient deficiencies in the soil and salt spray, making leaf renewal necessary (Pires *et al.* 2006b). Thus, the continuous production of leaves should ensure the constant maintenance of photosynthetic rates (Pires *et al.* 2006b).

Myrcia ovina exhibits an annual flowering pattern, with no observed second reproductive cycle within the 12-month study period. This suggests a single, yearly reproductive event, which is consistent with patterns frequently documented in the Myrtaceae family and common in Restinga ecosystems (Marques & Oliveira 2004a, Covre & Guerra 2016), as well as in other ecologically important families in these environments, such as Melastomataceae (F. D. S. Oliveira *et al.* 2016, V. L. G. Brito *et al.* 2017) and Rubiaceae (Andrade *et al.* 2020). However, since this conclusion is based on a one-year sampling period, our ability to detect interannual variability or irregular flowering events is limited. Environmental factors such as temperature and rainfall may also influence flowering

time. Therefore, a longer sampling period would enhance our understanding of the long-term reproductive phenology of this species.

Bud sprouting and flowering were seasonal events that predominantly occurred during the dry season and at relatively high temperatures, up to the beginning of the rainy season, when temperatures start to decrease, with few individuals blooming beyond this period. This is a common pattern in native species of Restingas (de Medeiros *et al.* 2007) and is more pronounced in canopy species (Marques & Oliveira 2004b), although flowering in the rainy season is also found in some Restinga communities (I. C. S. Machado *et al.* 1997, Araújo Rodarte *et al.* 2022) and is common in some other communities (Ferreira *et al.* 2024). Flowering during the dry season was early recognized as one of the dominant patterns in Myrtaceae (Lughadha & Proenca 1996), being described for species such as *Myrcia splendens* (Sw.) DC. in the Restingas of state of Ceara, Northeast Brazil (Cunha *et al.* 2016), and is also present in other important families of the Restinga flora, such as Sapotaceae (Gomes *et al.* 2008) and Arecaceae (Mendes *et al.* 2016). In contrast, *Myrcia ilheosensis* Kiaersk, *Myrcia loranthifolia* (DC.) G.P. Burton & E. Lucas and *Myrcia vittoriana* Kiaersk flowered at similar times but when the climate was warmer and wetter (Medeiros & Haiad 2022). In an ecological context, this flowering pattern may represent an efficient strategy to avoid the peaks of floral herbivory observed during the rainy season (Rathcke & Lacey 1985). In the Restinga ecosystems of Sergipe and Ceará states, in Northeast Brazil, the rainy season typically occurs between April and July and is characterized by high humidity and dense vegetative growth. Our phenological data show that *Myrcia ovina* tends to flower primarily during the dry and warm seasons, with reduced flowering activity during peak rainfall months. By flowering at the margins of the rainy season, *Myrcia ovina* may reduce exposure to florivores, whose abundance and activity increase under wetter conditions (Aide 1992). Additionally, flowering outside the rainiest months may help avoid damage to floral structures and reduce pollen viability caused by high humidity and direct rain impact (Galen 2005).

Interestingly, this seasonal flowering pattern contrasts with observations in Southeastern Brazil (e.g., São Paulo and Rio de Janeiro), where *Myrcia* species tend to flower during periods that are both warmer and wetter, typically aligning with the summer rainy season. This regional variation raises the question of whether flowering in *Myrtaceae* is more strongly influenced by temperature (i.e., summer) or by seasonal rainfall patterns. In Southeast Brazil, flowering seems to coincide with higher temperatures and abundant moisture, whereas in Northeast Brazil, *Myrcia ovina* appears to respond more to dry and warm conditions. These patterns suggest that different species or populations of *Myrtaceae* may adopt distinct phenological strategies depending on local climatic regimes, possibly balancing factors such as pollinator availability, floral herbivory, and abiotic stressors.

From a competition perspective, variability in flowering patterns, such as species flowering during the dry season, can reduce interspecific competition for pollinators, minimize pollen loss, prevent the clogging of stigmas with heterospecific pollen, and even lower the risk of forming infertile hybrids. This strategy may be especially important in ecosystems with high *Myrtaceae* species richness, such as the Restingas of Northeastern Brazil, where species often share similar floral morphology and pollination systems (Vasconcelos *et al.* 2019) and several are known to hybridize (Ebbehøj & Thomsen 1991). Our data show that *Myrcia ovina* follows a distinct phenological pattern in this context, flowering predominantly during the dry and warm seasons, whereas many other *Myrtaceae* in the same habitats flower during wetter periods (personal observation). This asynchrony likely functions as a temporal niche differentiation mechanism, reducing overlap with closely related species and lessening interspecific reproductive interference. This interpretation is supported by the negative correlation we found between bud and flower production and monthly precipitation. Importantly, from the perspective of pollinator availability, *M. ovina* does not appear to face challenges during the dry season, as bees — the primary pollinators for *Myrtaceae* — remain abundant year-round and may even increase in number during dry periods (Kamke *et al.* 2011). In contrast, in Southeastern Brazil, where climate regimes and community compositions differ, many

Myrcia species and other Myrtaceae flower during the warm and rainy seasons — a period of high pollinator activity but also greater competition.

Thus, the dry season flowering of *M. ovina* may be understood as an adaptive strategy that helps avoid both abiotic constraints (e.g., rainfall damage) and biotic pressures (e.g., pollinator competition and hybridization risk). A correlation was observed between bud sprouting and precipitation in the previous months. This may represent an effect of past precipitation on the bud sprouting, stemming from that period of greater resource availability. For example, the additional moisture provided by precipitation can increase the bioavailability of nutrients in the soil (Comerford 2005), such as potassium, calcium, and magnesium (Scheer 2011), which play important roles in floral development (Loka *et al.* 2019). Rainfall is a well-known inducer of reproductive phenology in tropical plants. Studies have associated increased soil moisture with the production of buds and flowers (Opler *et al.* 1976). This increase in water availability for plants in the upper layers of the soil (Antunes *et al.* 2019) requires less energy to capture this resource, which could represent an advantage during reproductive periods, as a constant influx of water is necessary to prevent the abortion of these flowers (Galen 2005).

However, in Restinga environments, such as those in Sergipe and other parts of coastal Northeast Brazil, the soils are typically sandy, nutrient-poor, and highly permeable (Scarano 2002), resulting in rapid drainage and reduced water retention. These characteristics may weaken or alter the relationship between rainfall and reproductive activity, which is commonly observed in more mesic tropical ecosystems. In such substrates, only species that can rapidly exploit short-term increases in soil moisture or that possess physiological adaptations to drought may successfully initiate reproduction during or after rain events (Lourenço *et al.* 2021). Thus, while rainfall may still act as a phenological cue in Restinga vegetation, its effect is likely more transient, species-specific, and mediated by edaphic conditions.

Environmental cues such as photoperiod and temperature also play key roles in shaping flowering patterns. Photoperiod influences flowering by breaking dormancy and promoting bud development (Opler *et al.* 1976). Although changes in day length are well-documented as triggers in South and Southeast Brazil (e.g., Araucaria Forest; Marques *et al.* 2004), recent studies have shown that even in tropical regions with minimal day length variation, slight changes can strongly affect plant reproduction (Davis *et al.* 2022b). Recognizing photoperiod as a driver of phenological variation highlights its importance in enabling plants to partition niches in space and time, thereby optimizing resource use (Jordan 2006). In parallel, flowering is strongly correlated with temperature: relatively high temperatures increase plant metabolism, photosynthesis, and nutrient uptake, providing the energy and resources necessary for reproduction — a response particularly evident in woody plants (Capovilla *et al.* 2015, Li *et al.* 2016, Fonseca *et al.* 2024).

Immature fruits occurred at the end of the dry season, and mature fruits extended into the early months of the rainy season, a reproductive pattern common in the Atlantic Forest (Dalponte & Lima 1999). Fruiting events are often seasonal, and this is the most common pattern in the genus *Myrcia* and is likely the most widespread in the Myrtaceae family (Marques & Oliveira 2004b, Marchioretto *et al.* 2007). Clearly, even among *Myrtaceae* species, there is great diversity in strategies and species interactions with environmental conditions, as shown by Staggemeier *et al.* (2007), who identified species that fruit at different times of the year in the Atlantic Forest of Cardoso Island, state of São Paulo.

During the rainy season, fruits and seeds are more abundant and nutritionally richer (Worman & Chapman 2005). While competition for bird dispersers may increase during the rainy season, Myrtaceae species have morphological and chemical traits that increase attraction and dispersal chances, for example, the fruits of *Myrcia ovina* are typically orange and red during the early and middle stages of maturation and then return to the late stages. Additionally, some species possess

complex chemical compositions—including carbohydrates, lipids, proteins, minerals, and vitamins—that likely influence bird fruit preferences (Stiles 1993).

Recent precipitation correlations suggest that excessive rainfall may hinder fruit maturation, as high moisture can promote fungal diseases and waterlogged soils, stress plants and affect mature fruit production (Tyagi *et al.* 2024). Conversely, the strong positive correlation with historical precipitation indicates that consistent moisture levels benefit plant health and productivity, increasing the likelihood of fruit maturation (Gorton *et al.* 2019). Temperature is another critical factor influencing fruiting. Higher temperatures can accelerate growth and maturation processes in fruit-bearing plants (Reddy *et al.* 1991). A research reported that distinct changes in air temperature can lead to clear responses in plant phenology, including the timing of fruit maturation (Kimura *et al.* 2009).

Reproductive cycles can also be correlated with soil nutrient availability (Scheer 2011), as the rainy season enhances seed germination and seedling survival (Garwood 1983). However, ornithochoric species may encounter disperser limitations due to changing bird compositions, with insectivorous species outnumbering frugivores. This shift can hinder reproductive success by reducing effective seed dispersal rates, creating a temporal mismatch between fruiting and frugivorous bird availability (Almeida *et al.* 2023).

In conclusion, *Myrcia ovina* exhibits unique ecological and reproductive strategies adapted to the challenging conditions of the Restinga ecosystem. Its evergreen nature facilitates continuous photosynthesis in nutrient-poor soils, increasing resilience. The species flowers annually during the dry season to avoid herbivory and coincide with pollinator availability. Its fruiting pattern, which extends into the early rainy season, maximizes seed dispersal despite competition, although excessive rainfall can hinder fruit maturation. This study underscores the influence of climatic factors and ecological interactions on reproductive strategies, offering vital insights for conservation efforts in critically endangered Restinga habitats. Understanding these relationships is essential for informing

conservation policies amidst increasing anthropogenic pressures, ensuring the persistence of biodiversity and ecosystem services.

ACKNOWLEDGMENTS

We would like to thank CNPq for providing the scientific initiation scholarship to the first author; the Transport Division of the Federal University of Sergipe for support during field activities; ICMBio and the management of the Private Natural Heritage Reserve Dona Benta and Seu Caboclo for granting permission to conduct fieldwork; and the ASE Herbarium team at the Federal University of Sergipe for their assistance in processing and incorporating specimens into the herbarium collection.

REFERENCES

- Abernethy, K., Bush, E. R., Forget, P.-M., Mendoza, I., & Morellato, L. P. C. 2018. Current issues in tropical phenology: a synthesis. *Biotropica*, 50(3), 477–482. DOI: 10.1111/btp.12558
- Aide, T. M. 1992. Dry Season Leaf Production: An Escape from Herbivory. *Biotropica*, 24(4), 532–537. DOI: 10.2307/2389016
- Almeida, B. A., Bochio, G. M., Calsavara, L. C., Marques, F. C., & dos Anjos, L. 2023. Seasonality in niche occupation revealed through bird community functional structure in the southern Atlantic rainforest. *Ibis*, 165(3), 986–997. DOI: 10.1111/ibi.13189
- Alvares, C. A., Stape, J. L., Sentelhas, P. C., De Moraes Gonçalves, J. L., & Sparovek, G. 2013. Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift*, 22(6), 711–728. DOI: 10.1127/0941-2948/2013/0507

- Alves, J. G. dos S., Santos, L. L. dos, Pereira-Silva, R. A., & Melo, A. L. de. 2024. Synopsis of *Myrcia* (Myrtaceae) in the State of Pernambuco, Brazil. *Biota Neotropica*, 24, e20231578. DOI: <https://doi.org/10.1590/1676-0611-BN-2023-1578>
- Andrade, L. K. F., Neto, E. R. S., Sá, T., & Quirino, Z. G. M. 2020. Fenologia reprodutiva de Rubiaceae juss. Na Mata Atlântica Paraibana. *Oecologia Australis*, 24(4), 848. DOI: [10.4257/oeco.2020.2404.07](https://doi.org/10.4257/oeco.2020.2404.07)
- Antunes, C., Silva, C., Máguas, C., Joly, C. A., & Vieira, S. 2019. Seasonal changes in water sources used by woody species in a tropical coastal dune forest. *Plant and Soil*, 437(1), 41–54. DOI: [10.1007/s11104-019-03947-9](https://doi.org/10.1007/s11104-019-03947-9)
- Araújo Rodarte, A. T., Benevides, C. R., Moreira, M. M., Greco, A. V., Leão, L. C. S., de Oliveira, P., Medeiros, T. Á., & de Lima, H. A. 2022. Flowering Phenology in a Restinga Community: 7 Years of Study. In: M. F. T. Medeiros & B. de Sá Haiad (Eds.), *Aspects of Brazilian Floristic Diversity : From Botany to Traditional Communities*. pp. 3–45. Cham: Springer International Publishing.
- Bencke, C. S. C., & Morellato, L. P. C. 2002. Estudo comparativo da fenologia de nove espécies arbóreas em três tipos de floresta atlântica no sudeste do Brasil. *Brazilian Journal of Botany*, 25, 237–248. DOI: <https://doi.org/10.1590/S0100-84042002000200012>
- Bezerra, R. H. S., & Bocchiglieri, A. 2021. Bats in a restinga area in Sergipe, Northeastern Brazil. *Papéis Avulsos de Zoologia*, 61, e20216131–e20216131. DOI: [10.11606/1807-0205/2021.61.31](https://doi.org/10.11606/1807-0205/2021.61.31)
- Bezerra-Silva, A., Albuquerque-Lima, S., Gomes, V. G. N., Fagundes, A. C. de A., Gomes, M. T. D., Silva, M. T. da, Machado, I. C., & Funch, L. S. 2024. When Are Cacti Found with Flowers and Fruits? Estimation of the Reproductive Phenology of the Genus *Xiquexique* Based on Herbarium Data. *Diversity*, 16(2), 79. DOI: [10.3390/d16020079](https://doi.org/10.3390/d16020079)

- Blonder, B., Both, S., Coomes, D. A., Elias, D., Jucker, T., Kvasnica, J., Majalap, N., Malhi, Y. S., Milodowski, D., Riutta, T., & Svátek, M. 2018. Extreme and Highly Heterogeneous Microclimates in Selectively Logged Tropical Forests. *Frontiers in Forests and Global Change*, 1. DOI: 10.3389/ffgc.2018.00005
- Borchert, R., Renner, S. S., Calle, Z., Navarrete, D., Tye, A., Gautier, L., Spichiger, R., & Von Hildebrand, P. 2005. Photoperiodic induction of synchronous flowering near the Equator. *Nature*, 433(7026), 627–629. DOI: 10.1038/nature03259
- Brito, L. da S., Irmiler, U., Forte, B. V. G., Xavier, T. P., & Martins, R. L. 2018. Matter turnover in the oligotrophic restinga ecosystem and the importance of the key species *Clusia hilariana*. *Biota Neotropica*, 18, e20180552. DOI: <https://doi.org/10.1590/1676-0611-BN-2018-0552>
- Brito, V. L. G., Maia, F. R., Silveira, F. A. O., Fracasso, C. M., Lemos-Filho, J. P., Fernandes, G. W., Goldenberg, R., Morellato, L. P. C., Sazima, M., & Staggemeier, V. G. 2017. Reproductive phenology of Melastomataceae species with contrasting reproductive systems: contemporary and historical drivers. *Plant Biology*, 19(5), 806–817. DOI: 10.1111/plb.12591
- Camara, R., Pereira, M. G., Menezes, L. F. T., Segall, A. B., & Castro, J. S. R. 2018. Litter Dynamics in a Forest Dune at Restinga da Marambaia, RJ, Brazil. *Floresta e Ambiente*, 25, e20160046. DOI: 10.1590/2179-8087.004616
- Canale, G. R., Suscke, P., Rocha-Santos, L., Bernardo, C. S. S., Kierulff, M. C. M., & Chivers, D. J. 2016. Seed Dispersal of Threatened Tree Species by a Critically Endangered Primate in a Brazilian Hotspot. DOI: 10.1159/000447712
- Capovilla, G., Schmid, M., & Posé, D. 2015. Control of flowering by ambient temperature. *Journal of Experimental Botany*, 66(1), 59–69. DOI: 10.1093/jxb/eru416
- Caselli, C. B., & Setz, E. Z. F. 2011. Feeding ecology and activity pattern of black-fronted titi monkeys (*Callicebus nigrifrons*) in a semideciduous tropical forest of southern Brazil. *Primates*, 52(4), 351–359. DOI: 10.1007/s10329-011-0266-2

- Chapman, C. A., Valenta, K., Bonnell, T. R., Brown, K. A., & Chapman, L. J. 2018. Solar radiation and ENSO predict fruiting phenology patterns in a 15-year record from Kibale National Park, Uganda. *Biotropica*, 50(3), 384–395. DOI: 10.1111/btp.12559
- Comerford, N. B. 2005. Soil Factors Affecting Nutrient Bioavailability. In: H. BassiriRad (Ed.), *Nutrient Acquisition by Plants: An Ecological Perspective*. pp. 1–14. Berlin, Heidelberg: Springer.
- Covre, C., & Guerra, T. M. 2016. Espécies melitófilas da restinga do Parque Estadual Paulo César Vinha, Espírito Santo, Brasil. Version 2. *Boletim Do Museu de Biologia Mello Leitao. Nova Serie*, 38(2), 73–90.
- Cunha, L. L. T., Lucena, E. M. P. de, & Bonilla, O. H. 2016. Exigências Térmicas da Floração à Frutificação de Espécies de Myrtaceae em Ambiente de Restinga (Thermal Requirements of Flowering to Fruiting of Species of Myrtaceae in Restinga Environment). Version 3. *Revista Brasileira de Geografia Física*, 9(3), 707–721. DOI: 10.26848/rbgf.v9.3.p707-721
- Dalponete, J. C., & Lima, E. D. S. 1999. Disponibilidade de frutos e a dieta de *Lycalopex vetulus* (Carnivora - Canidae) em um cerrado de Mato Grosso, Brasil. *Brazilian Journal of Botany*, 22, 325–332. DOI: 10.1590/S0100-84041999000500015
- Davies, T. J., Wolkovich, E. M., Kraft, N. J. B., Salamin, N., Allen, J. M., Ault, T. R., Betancourt, J. L., Bolmgren, K., Cleland, E. E., Cook, B. I., Crimmins, T. M., Mazer, S. J., McCabe, G. J., Pau, S., Regetz, J., Schwartz, M. D., & Travers, S. E. 2013. Phylogenetic conservatism in plant phenology. *Journal of Ecology*, 101(6), 1520–1530. DOI: 10.1111/1365-2745.12154
- Davis, C. C., Lyra, G. M., Park, D. S., Asprino, R., Maruyama, R., Torquato, D., Cook, B. I., & Ellison, A. M. 2022a. New directions in tropical phenology. *Trends in Ecology & Evolution*, 37(8), 683–693. DOI: 10.1016/j.tree.2022.05.001

- Davis, C. C., Lyra, G. M., Park, D. S., Asprino, R., Maruyama, R., Torquato, D., Cook, B. I., & Ellison, A. M. 2022b. New directions in tropical phenology. *Trends in Ecology & Evolution*, 37(8), 683–693. DOI: 10.1016/j.tree.2022.05.001
- de Medeiros, D. P. W., Lopes, A. V., & Zickel, C. S. 2007. Phenology of woody species in tropical coastal vegetation, northeastern Brazil. *Flora - Morphology, Distribution, Functional Ecology of Plants*, 202(7), 513–520. DOI: 10.1016/j.flora.2006.11.002
- Dos Santos Ferreira, B. H., Da Rosa Oliveira, M., Mariano Fernandes, R. A., Fujizawa Nacagava, V. A., Arguelho, B. A., Ribeiro, D. B., Pott, A., Damasceno Junior, G. A., & Garcia, L. C. 2023. Flowering and fruiting show phenological complementarity in both trees and non-trees in mosaic-burnt floodable savanna. *Journal of Environmental Management*, 337, 117665. DOI: 10.1016/j.jenvman.2023.117665
- dos Santos-Neto, A. dos S., Oliveira, E. V. da S., Faiad, P. J. B., & Landim, M. F. 2024. O pastejo afeta a estrutura da vegetação herbácea de restinga? Uma análise nos campos abertos inundáveis da Reserva Biológica de Santa Isabel, Litoral Norte de Sergipe. Version 2. *Biodiversidade Brasileira*, 14(2), 121–132. DOI: 10.37002/biodiversidadebrasileira.v14i2.2482
- dos Santos-Neto, A. M. dos, Oliveira, E. V. da S., Faiad, P. J. B., & Landim, M. F. 2018. Sazonalidade e estrutura da vegetação herbácea de Restingas: uma análise na Reserva Biológica de Santa Isabel, SE. *Brazilian Journal of Ecology*, 1, 1–21.
- Ebbehøj, K. F., & Thomsen, P. D. 1991. Differentiation of closely related species by DNA hybridization. *Meat Science*, 30(4), 359–366. DOI: 10.1016/0309-1740(91)90044-Q
- Elhalawany, A. S., & Abou-Setta, M. M. 2013. Mites Inhibiting Guava Trees and Their Dynamics in Relation to Weather Factors and Plant Phenology. *Acarines: Journal of the Egyptian Society of Acarology*, 7(2), 17–21. DOI: 10.21608/ajesa.2013.163685

- Ferreira, B. H. S., Freitas, T. G., Arakaki, L. M. M., Covre, W. S., Damasceno-Junior, G. A., Galetto, L., & Sigrist, M. R. 2024. Vegetative and reproductive phenology in seasonal climate vegetation: phenological complementarity between woody and herbaceous plants in the Brazilian Chaco. *Flora*, 316, 152520. DOI: 10.1016/j.flora.2024.152520
- Fonseca, R. B. S., Nunes, E. M. B., Costa, J. S. da, Menezes, I. S., Miranda, L. d'Afonseca P. de, Borba, E. L., & Funch, L. S. 2024. Myrtaceae flowering strategies in a gallery forest, Chapada Diamantina, Brazil. *Rodriguésia*, 75, e00042023. DOI: <https://doi.org/10.1590/2175-7860202475042>
- Fournier, L. 1974. Un método cuantitativo para la medición de características fenológicas em árboles. *Turrialba*, (24), 422–423.
- Galen, C. 2005. 3 - It Never Rains but then it Pours: The Diverse Effects of Water on Flower Integrity and Function. In: E. G. Reekie & F. A. Bazzaz (Eds.), *Reproductive Allocation in Plants*. pp. 77–95. Burlington: Academic Press.
- Gao, F., & Zhang, X. 2021. Mapping Crop Phenology in Near Real-Time Using Satellite Remote Sensing: Challenges and Opportunities. *Journal of Remote Sensing*, 2021. DOI: 10.34133/2021/8379391
- Garwood, N. C. 1983. Seed Germination in a Seasonal Tropical Forest in Panama: A Community Study. *Ecological Monographs*, 53(2), 159–181. DOI: 10.2307/1942493
- Gentry, A. H. 1974. Flowering Phenology and Diversity in Tropical Bignoniaceae. *Biotropica*, 6(1), 64–68. DOI: 10.2307/2989698
- Gomes, R., Pinheiro, M. C. B., & Lima, H. A. de. 2008. Fenologia reprodutiva de quatro espécies de Sapotaceae na restinga de Maricá, RJ. *Brazilian Journal of Botany*, 31, 679–687. DOI: 10.1590/S0100-84042008000400013

- Gong, Z., Ge, W., Guo, J., & Liu, J. 2024. Satellite remote sensing of vegetation phenology: Progress, challenges, and opportunities. *ISPRS Journal of Photogrammetry and Remote Sensing*, 217, 149–164. DOI: 10.1016/j.isprsjprs.2024.08.011
- Gorton, A. J., Tiffin, P., & Moeller, D. A. 2019. Does adaptation to historical climate shape plant responses to future rainfall patterns? A rainfall manipulation experiment with common ragweed. *Oecologia*, 190(4), 941–953. DOI: 10.1007/s00442-019-04463-4
- Gray, R. E. J., & Ewers, R. M. 2021. Monitoring Forest Phenology in a Changing World. Version 3. *Forests*, 12(3), 297. DOI: 10.3390/f12030297
- Hijmans, R. J. 2018. raster: Geographic data analysis and modeling. R Package Version, 2.8. Available on: <https://CRAN.R-project.org/package=raster>.
- IUCN. 2018. *Myrcia ovina*: Canteiro, C., Lima, D. & Lucas, E.: The IUCN Red List of Threatened Species 2019: e.T122657325A122659317. DOI: 10.2305/IUCN.UK.2019-2.RLTS.T122657325A122659317.en
- Jordan, B. R. 2006. *The Molecular Biology and Biotechnology of Flowering*. Wallingford, UK: CABI Publishing: p. 404.
- Kamke, R., Zillikens, A., & Steiner, J. 2011. Species richness and seasonality of bees (Hymenoptera, Apoidea) in a restinga area in Santa Catarina, southern Brazil. *Studies on Neotropical Fauna and Environment*, 46(1), 35–48. DOI: 10.1080/01650521.2010.538561
- Kimura, K., Yumoto, T., Kikuzawa, K., & Kitayama, K. 2009. Flowering and fruiting seasonality of eight species of *Medinilla* (Melastomataceae) in a tropical montane forest of Mount Kinabalu, Borneo. *Tropics*, 18(1), 35–44. DOI: 10.3759/tropics.18.35
- Li, L., Li, X., Liu, Y., & Liu, H. 2016. Flowering responses to light and temperature. *Science China Life Sciences*, 59(4), 403–408. DOI: 10.1007/s11427-015-4910-8

- Lima, D. F. D. S. 2017. Estudos filogenéticos e taxonômicos em *Myrcia* DC. sensu lato (Myrtaceae), com ênfase no clado Guianensis. Doctoral thesis. Universidade Estadual de Campinas. p. 334. Retrieved from <https://repositorio.unicamp.br/Busca/Download?codigoArquivo=486593>
- Loka, D. A., Oosterhuis, D. M., Baxevanos, D., Vlachostergios, D., & Hu, W. 2019. How potassium deficiency alters flower bud retention on cotton (*Gossypium hirsutum* L.). *Archives of Agronomy and Soil Science*, 65(4), 521–536. DOI: 10.1080/03650340.2018.1511894
- Lourenço, J., Newman, E. A., Ventura, J. A., Milanez, C. R. D., Thomaz, L. D., Wandekoken, D. T., & Enquist, B. J. 2021. Soil-associated drivers of plant traits and functional composition in Atlantic Forest coastal tree communities. *Ecosphere*, 12(7), e03629. DOI: 10.1002/ecs2.3629
- Lughadha, E. N., & Proenca, C. 1996. A Survey of the Reproductive Biology of the Myrtoideae (Myrtaceae). *Annals of the Missouri Botanical Garden*, 83(4), 480–503. DOI: 10.2307/2399990
- Lund, U., Agostinelli, C., Arai, H., Gagliardi, A., García-Portugués, E., Giunchi, D., Irisson, J.-O., Pocernich, M., & Rotolo, F. 2024, August 29. circular: Circular Statistics.0.5-1 (Version 0.5-1).
- Machado, I. C. S., Barros, L. M., & Sampaio, E. V. S. B. 1997. Phenology of Caatinga Species at Serra Talhada, PE, Northeastern Brazil. *Biotropica*, 29(1), 57–68. DOI: 10.1111/j.1744-7429.1997.tb00006.x
- Machado, W. de J. 2018. Fenologia da vegetação em áreas de Areias Brancas no Parque Nacional Serra de Itabaiana, Sergipe, Brasil.
- Marchioretto, M. S., Mauhs, J., & Budke, J. C. 2007. Fenologia de espécies arbóreas zoocóricas em uma floresta psamófila no sul do Brasil. *Acta Botanica Brasilica*, 21, 193–201. DOI: 10.1590/S0102-33062007000100018

- Marques, M. C. M., & Oliveira, P. E. A. M. 2004a. Fenologia de espécies do dossel e do sub-bosque de duas Florestas de Restinga na Ilha do Mel, sul do Brasil. *Brazilian Journal of Botany*, 27, 713–723. DOI: <https://doi.org/10.1590/S0100-84042004000400011>
- Marques, M. C. M., & Oliveira, P. E. A. M. 2004b. Fenologia de espécies do dossel e do sub-bosque de duas Florestas de Restinga na Ilha do Mel, sul do Brasil. *Brazilian Journal of Botany*, 27, 713–723. DOI: [10.1590/S0100-84042004000400011](https://doi.org/10.1590/S0100-84042004000400011)
- Marques, M. C. M., Roper, J. J., & Baggio Salvalaggio, A. P. 2004. Phenological patterns among plant life-forms in a subtropical forest in southern Brazil. *Plant Ecology*, 173(2), 203–213. DOI: [10.1023/B:VEGE.0000029325.85031.90](https://doi.org/10.1023/B:VEGE.0000029325.85031.90)
- Medeiros, M. F. T., & Haiad, B. de S. 2022. Aspects of Brazilian Floristic Diversity: From Botany to Traditional Communities. Cham: Springer Nature: p. 292.
- Melo, J. D. D. O., Stadnik, A. M. S., & Roque, N. 2023. Myrtaceae Juss. in restinga of Bahia: diversity, taxonomy, and distribution. *Acta Botanica Brasilica*, 37, e20220194. DOI: [10.1590/1677-941x-abb-2022-0194](https://doi.org/10.1590/1677-941x-abb-2022-0194)
- Mendes, F. N., Valente, R. M., Rêgo, M. M. C., & Esposito, M. C. 2016. Reproductive phenology of *Mauritia flexuosa* L. (Arecaceae) in a coastal restinga environment in northeastern Brazil. *Brazilian Journal of Biology*, 77, 29–37. DOI: [10.1590/1519-6984.08515](https://doi.org/10.1590/1519-6984.08515)
- Menzel, A., Yuan, Y., Matiu, M., Sparks, T., Scheifinger, H., Gehrig, R., & Estrella, N. 2020. Climate change fingerprints in recent European plant phenology. *Global Change Biology*, 26(4), 2599–2612. DOI: [10.1111/gcb.15000](https://doi.org/10.1111/gcb.15000)
- Morellato, L. P. C., Rodrigues, R. R., Leitao Filho, H. F., & Joly, C. A. 1989. Estudo comparativo da fenologia de espécies arbóreas de floresta de altitude e floresta mesofila semidecidua na serra do Japi, Jundiaí, São Paulo. *Revista Brasileira de Botânica*, 12, 85–98.
- Morellato, L. Patricia C., Alberti, L. F., & Hudson, I. L. 2010. Applications of Circular Statistics in Plant Phenology: a Case Studies Approach. In: I. L. Hudson & M. R. Keatley (Eds.),

- Phenological Research: Methods for Environmental and Climate Change Analysis. pp. 339–359. Dordrecht: Springer Netherlands.
- Newstrom, L. E., Frankie, G. W., & Baker, H. G. 1994. A New Classification for Plant Phenology Based on Flowering Patterns in Lowland Tropical Rain Forest Trees at La Selva, Costa Rica. *Biotropica*, 26(2), 141–159. DOI: 10.2307/2388804
- Oliveira, E. V. da S., Ferreira Sobrinho, E. dos S., & Landim, M. F. 2015. Flora from the restingas of Santa Isabel Biological Reserve, northern coast of Sergipe state, Brazil. *Check List*.
- Oliveira, E. V. da S., & Landim, M. F. 2020. Dunes in the North coast of Sergipe, Brazil: plant species and their ecological traits. *Rodriguésia*, 71, e01242018. DOI: 10.1590/2175-7860202071021
- Oliveira, E. V. S., & Landim, M. F. 2014. Caracterização fitofisionômica das restingas da Reserva Biológica de Santa Isabel, litoral norte de Sergipe. Version 10. *Scientia Plena*, 10(10).
- Oliveira, F. D. S., Ribeiro, M. H. M., Nunez, C. V., & Albuquerque, P. M. C. D. 2016. Flowering phenology of *Mouriri guianensis* (Melastomataceae) and its interaction with the crepuscular bee *Megalopta amoena* (Halictidae) in the restinga of Lençóis Maranhenses National Park, Brazil. *Acta Amazonica*, 46(3), 281–290. DOI: 10.1590/1809-4392201504853
- Opler, P. A., Frankie, G. W., & Baker, H. G. 1976. Rainfall as a Factor in the Release, Timing, and Synchronization of Anthesis by Tropical Trees and Shrubs. *Journal of Biogeography*, 3(3), 231–236. DOI: 10.2307/3038013
- Park, D. S., Lyra, G. M., Ellison, A. M., Maruyama, R. K. B., dos Reis Torquato, D., Asprino, R. C., Cook, B. I., & Davis, C. C. 2023. Herbarium records provide reliable phenology estimates in the understudied tropics. *Journal of Ecology*, 111(2), 327–337. DOI: 10.1111/1365-2745.14047
- Pires, L. A., Britez, R. M. de, Martel, G., & Pagano, S. N. 2006a. Produção, acúmulo e decomposição da serapilheira em uma restinga da Ilha do Mel, Paranaguá, PR, Brasil. *Acta Botanica Brasilica*, 20, 173–184. DOI: <https://doi.org/10.1590/S0102-33062006000100016>

- Pires, L. A., Britez, R. M. de, Martel, G., & Pagano, S. N. 2006b. Produção, acúmulo e decomposição da serapilheira em uma restinga da Ilha do Mel, Paranaguá, PR, Brasil. *Acta Botanica Brasilica*, 20, 173–184. DOI: 10.1590/S0102-33062006000100016
- Proenca, C. E., Oliveira, M. I. U., Sobral, M., & Landim, M. F. 2014. Novelties in Myrtaceae: contributions to the Flora of the State of Sergipe, Brazil. *Phytotaxa*, 173(3), 217–225.
- Rathcke, B., & Lacey, E. P. 1985. Phenological Patterns of Terrestrial Plants. *Annual Review of Ecology and Systematics*, 16(1), 179–214. DOI: 10.1146/annurev.es.16.110185.001143
- R Core Team (2022). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Reddy, V. R., Reddy, K. R., & Baker, D. N. 1991. Temperature Effect on Growth and Development of Cotton During the Fruiting Period. *Agronomy Journal*, 83(1), 211–217. DOI: 10.2134/agronj1991.00021962008300010050x
- Sakai, S., & Kitajima, K. 2019. Tropical phenology: Recent advances and perspectives. *Ecological Research*, 34(1), 50–54. DOI: 10.1111/1440-1703.1131
- San Martin-Gajardo, I., & Morellato, L. P. C. 2003. Fenologia de Rubiaceae do sub-bosque em floresta Atlântica no sudeste do Brasil. *Brazilian Journal of Botany*, 26, 299–309. DOI: 10.1590/S0100-84042003000300003
- Santos, P. L., & Ferreira, R. A. 2013. Fenologia de *Tapirira guianensis* AUBL. (Anacardiaceae) no município de São Cristóvão, Sergipe. *Revista Árvore*, 37, 129–136. DOI: 10.1590/S0100-67622013000100014
- SCARANO, F. R. 2002. Structure, Function and Floristic Relationships of Plant Communities in Stressful Habitats Marginal to the Brazilian Atlantic Rainforest. *Annals of Botany*, 90(4), 517–524. DOI: 10.1093/aob/mcf189

- Scheer, M. B. 2011. Mineral nutrient fluxes in rainfall and throughfall in a lowland Atlantic rainforest in southern Brazil. *Journal of Forest Research*, 16(1), 76–81. DOI: 10.1007/s10310-010-0222-9
- Souza, S., Tomasella, J., Gracia, M., Amorim, Ma., Menezes, P., & Pinto, C. 2001. O Programa de Monitoramento Climatico em Tempo Real na area de atuacao da SUDENE PROCLIMA. *Bol. Soc. Bras. Meteor.*, 25.
- Ssali, F., & Sheil, D. 2023. Seasonality in the equatorial tropics: Flower, fruit, and leaf phenology of montane trees in the highlands of Southwest Uganda. *Biotropica*, 55(3), 680–698. DOI: 10.1111/btp.13219
- Staggemeier, V. G., Morellato, L. P. C., & Galetti, M. 2007. Fenologia Reprodutiva de Myrtaceae em uma ilha continental de Floresta Atlântica. Version S1. *Revista Brasileira de Biociências*, 5(S1), 423–425.
- Stiles, E. W. 1993. The influence of pulp lipids on fruit preference by birds. In: T. H. Fleming & A. Estrada (Eds.), *Frugivory and seed dispersal: ecological and evolutionary aspects*. pp. 227–235. Dordrecht: Springer Netherlands.
- Talora, D. C., & Morellato, P. C. 2000. Fenologia de espécies arbóreas em floresta de planície litorânea do sudeste do Brasil. *Brazilian Journal of Botany*, 23, 13–26. DOI: 10.1590/S0100-84042000000100002
- Tyagi, A., Ali, S., Mir, R. A., Sharma, S., Arpita, K., Almalki, M. A., & Mir, Z. A. 2024. Uncovering the effect of waterlogging stress on plant microbiome and disease development: current knowledge and future perspectives. *Frontiers in Plant Science*, 15. DOI: 10.3389/fpls.2024.1407789
- Vasconcelos, T. N. C., Chartier, M., Prenner, G., Martins, A. C., Schönenberger, J., Wingler, A., & Lucas, E. 2019. Floral uniformity through evolutionary time in a species-rich tree lineage. *New Phytologist*, 221(3), 1597–1608. DOI: 10.1111/nph.15453

Worman, C. O., & Chapman, C. A. 2005. Seasonal variation in the quality of a tropical ripe fruit and the response of three frugivores. *Journal of Tropical Ecology*, 21(6), 689–697. DOI: 10.1017/S0266467405002725

Wright, S. J., & Calderón, O. 2006. Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. *Ecology Letters*, 9(1), 35–44. DOI: 10.1111/j.1461-0248.2005.00851.x

Submitted: 24 September 2024

Accepted: 23 September 2025

Published: 06 February 2026

Associate Editor: Amanda Souza dos Santos

Ahead of print