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Phenological seasonality and seed germination of *Copaifera martii* Hayne in the southeastern Amazon

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ABSTRACT

Among Amazonian tree species used for non-timber forest products, *Copaifera martii* Hayne (copaíba) is notable for its oleoresin, widely used in folk medicine, and for its seeds, which are essential for seedling production. Phenological studies improve our understanding of species dynamics and support effective forest management. This study, conducted in the Carajás National Forest, aimed to characterize the phenology of *C. martii*, correlate its phenophases with climatic factors, and assess seed germination potential. Twenty individuals were monitored monthly over two years for vegetative and reproductive phenophases. Germination tests were performed with seeds from four trees. *Copaifera martii* exhibited distinct phenological seasonality, with flowering peaking during the rainy season and fruiting concentrated in the dry season. New leaf emergence peaked at the rainy-to-dry transition; leaf fall peaked in the dry season with no defined seasonality. Among the phenophases, the production of new leaves, floral buds, and mature fruits was positively correlated with rainfall, while immature fruits were significantly associated with temperature variation. Seeds showed high germination rates. These findings support the creation of phenological calendars to guide sustainable seed harvesting and seedling production. They also provide ecological insights into the reproductive timing of *C. martii*, contributing to conservation and forest management strategies in Eastern Amazonia.

KEYWORDS: phenodynamic; extractivism; copaiba; Brazilian Amazon

Sazonalidade fenológica e germinação de sementes de *Copaifera martii* Hayne no sudeste da Amazônia

RESUMO

Entre as espécies arbóreas amazônicas utilizadas para produtos florestais não madeireiros, *Copaifera martii* Hayne (copaíba) se destaca por seu óleo-resina, amplamente empregado na medicina popular, e por suas sementes, essenciais para a produção de mudas. Estudos fenológicos aprimoram nossa compreensão da dinâmica das espécies e subsidiam estratégias eficazes de manejo florestal. Este estudo, realizado na Floresta Nacional de Carajás, teve como objetivo caracterizar a fenologia de *C. martii*, correlacionar suas fenofases com fatores climáticos e avaliar o potencial germinativo de suas sementes. Vinte indivíduos foram monitorados mensalmente durante dois anos para registros de fenofases vegetativas e reprodutivas. Testes de germinação foram realizados com sementes provenientes de quatro árvores. *Copaifera martii* apresentou marcada sazonalidade fenológica, com picos de floração durante a estação chuvosa e frutificação concentrada na estação seca. A emissão de novas folhas teve pico na transição do período chuvoso para o seco, enquanto a queda foliar ocorreu principalmente na estação seca, sem padrão sazonal definido. Dentre as fenofases, a produção de novas folhas, botões florais e frutos maduros correlacionou-se positivamente com a precipitação, enquanto os frutos imaturos foram significativamente associados à variação da temperatura. As sementes apresentaram alta taxa de germinação. Esses resultados apoiam a criação de calendários fenológicos para orientar a coleta sustentável de sementes e a produção de mudas, além de fornecerem subsídios ecológicos sobre o período reprodutivo de *C. martii*, contribuindo para estratégias de conservação e manejo florestal na Amazônia Oriental.

PALAVRAS-CHAVE: fenodinâmica; extrativismo; copaíba; Amazônia Brasileira

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INTRODUCTION

The Amazon rainforest holds great potential for the production of non-timber forest products (NTFPs), which have a wide range of applications, including in the food industry, medicine, fuel production, cosmetics, handicrafts, and the restoration of degraded areas (Pedrozo *et al.* 2017; Stevaux *et al.* 2022). The sustainable management of these resources supports the economies of many municipalities and constitutes a primary source of income for numerous traditional communities (Pinheiro *et al.* 2019), amid growing global interest in the development of techniques and technologies that sustain society while promoting the conservation of natural resources (Pinheiro *et al.* 2019).

Among the various Amazonian tree species used for obtaining NTFPs, *Copaifera martii* Hayne (one of the species known as copaíba) stands out. This species is highly valued for its broad range of applications in industry and cosmetics. The oleoresin extracted from copaíba has garnered particular attention for its medicinal properties, being widely used in traditional medicine for its anti-inflammatory and antibacterial effects. These characteristics make it a key ingredient in various folk remedies (Rosa and Gomes 2009; Vasconcelos *et al.* 2020; Costa and Lameira 2021; Nogueira *et al.* 2022).

In addition to its socioeconomic value, *C. martii* holds significant ecological relevance, particularly within the scope of forest restoration efforts. Given this dual importance, its potential use in reforestation programs highlights the need to understand its reproductive biology and seed germination behavior. This knowledge is especially important in regions affected by intense environmental degradation and extractive activities, such as southeastern Pará, where the Carajás region has historically undergone extensive forest exploitation driven by large-scale mining and logging (Fearnside 1989; Sonter *et al.* 2017). These activities not only increase pressure on natural resources but also give rise to legal requirements for environmental compensation and restoration. As a result, there is a growing demand for seeds of native tree species to supply forest nurseries and support restoration practices (ICMBio 2017). In this scenario, understanding the germination potential of seeds is fundamental for nursery operations, as it provides key insights into seed performance and viability (Bessa *et al.* 2015; Torres *et al.* 2020). Furthermore, since seed germination is closely linked to the plant's reproductive cycle - including flowering and fruiting periods - phenological data become essential for identifying optimal seed collection windows, thereby improving germination success rates, and enhancing seedling production efficiency.

To support seed collection efforts and improve understanding of reproductive dynamics such as germination potential, phenological analysis stands out as a valuable tool for assessing the reproductive dynamics of species. It provides essential information to guide management strategies aimed at harvesting forest resources with minimal impact on target species and overall forest dynamics (Calvi and Piña-Rodrigues 2016; Morellato *et al.* 2016; Buisson *et al.* 2017). Such studies also lay the groundwork for further research into reproductive biology, as well as the collection and dispersal of fruits and seeds (Costa and Lameira 2021). In this context, phenology refers to the study of biological cycle events (Costa and Lameira, 2021), which are influenced by biotic and abiotic factors, the latter mainly comprising climatic variables such as rainfall and temperature - likely the most significant drivers (Martins *et al.* 2019; Santana *et al.* 2020).

Phenological patterns in tropical ecosystems are strongly shaped by climatic factors, particularly rainfall and temperature, which regulate the availability of water and energy for reproductive processes (Cattanio *et al.* 2004; Girardin *et al.* 2016). Plants often evolve phenological strategies that synchronize reproductive events with periods of optimal environmental conditions, maximizing pollination success, primary productivity and seedling establishment (Primack 1987; Tannus *et al.* 2006; Belo *et al.* 2013; Pau *et al.* 2013). In this context, rainfall regimes play a central role, especially in regions with pronounced dry and wet seasons like southeastern Pará (Alvares *et al.* 2013; Martins *et al.* 2019; Santana *et al.* 2020). In the Carajás region, studies have shown that many shrub and herbaceous species exhibit seasonal reproductive behavior, likely shaped by these climatic cues (Scatigna *et al.* 2017; Costa *et al.* 2023). Specifically, *Copaifera* displays sensitivity to climatic variability, with reproductive events occurring at different times across its distribution depending on regional climatic regimes (Dias and Oliveira 1996; Braga *et al.* 2019). Such variability suggests that environmental triggers may influence not only phenological timing but also subsequent processes such as seed development and germination potential.

Understanding these links is particularly relevant because germination represents a critical phase in the plant life cycle and is often tightly controlled by climatic conditions during seed maturation and dispersal (Primack 1987; Segrestin *et al.* 2018). Variations in temperature and rainfall during these phases can influence seed viability, dispersion and emergence timing, reflecting in the success establishment (Primack 1987; Wolkovich and Cleland 2013; Braga *et al.* 2019). Yet, little is known about how these processes unfold specifically in *C. martii*, especially under the climatic regimes of Carajás, highlighting the need for targeted phenological and germination studies.

This study aimed to characterize the reproductive and vegetative phenology of *Copaifera martii*, correlate these patterns with climatic variables, and analyze the seed germination rate of tree individuals in dense ombrophilous forest formations within the Carajás National Forest (FLONA), in southeastern Pará State. The research sought to test the following hypotheses: (i)

Copaifera martii exhibits a seasonal reproductive phenological pattern, with specific reproductive phases (i.e. ripe fruits and seed dispersal) occurring predominantly during certain periods of the year; (ii) phenodynamics of *C. martii* are correlated with seasonal climatic variations, particularly rainfall, as an adaptive strategy to optimize reproductive success, and the interannual variability in precipitation and temperature will significantly influence the activity of reproductive events; and (iii) *Copaifera martii* monitored individuals produce seeds with high germination capacity.

MATERIAL AND METHODS

Study Area

The study was conducted in dense ombrophilous forest formations within the Carajás National Forest (FLONA), located in the southeastern part of the state of Pará, Brazil. The area is characterized by flat to gently undulating terrain. The predominant soil types in the area include Cambisols, Plinthosols, and Litholic Neosols, all with a gravelly texture (Santos *et al.* 2018). The climate is classified as "Aw" according to the Köppen system, featuring two well-defined seasons: a rainy summer (November to May) and a dry winter (June to October). Average temperatures range from 23°C to 26°C, with annual rainfall between 2,000 and 2,400 mm (Alvares *et al.* 2013). The research was duly authorized by the Sistema de Autorização e Informação em Biodiversidade (SISBIO, license number 78930-1).

Phenological monitoring

Phenological monitoring was conducted in three permanent rectangular plots of 2,000 m² each, located within the Carajás National Forest (FLONA). These plots - P9 (6°3'05.9"S; 50°16'48.3"W), P10 (6°3'34.2"S; 50°14'38.5"W) and P11 (6°4'31.2"S; 50°13'37.7"W) - are situated in the Serra Norte region, specifically near the N1 and N2 mining areas (iron ore extraction sites within the Carajás mining complex) (Figure 1). Twenty individuals of *C. martii* were selected based on forest inventory data, considering criteria such as good phytosanitary condition and clear canopy visibility, including individuals located adjacent to the permanent plots.

Monthly phenological monitoring was carried out from June 2021 to May 2023 to record both vegetative and reproductive phenophases, using binoculars to aid in the observations. Vegetative phases included leaf fall and the emergence of new leaves, while reproductive phases comprised flowering (flower buds and anthesis), fruiting (unripe and ripe fruits) and fruit dispersal, identified by the presence of open fruits exposed to dispersal agents such as wind, gravity or animals, following the criteria outlined by Morellato *et al.* (2000) and Belo *et al.* (2013).

Two phenological indices were evaluated to quantify these phases: intensity and activity. Phenophase intensity was estimated during field observations using a semi-quantitative scale for each individual (0 = absence of the phenophase; 1 = 1–25% occurrence; 2 = 26–50% occurrence; 3 = 51–75% occurrence; 4 = 76–100% occurrence), according to Fournier (1974). The activity index was based on the percentage of individuals within the population exhibiting a given phenological event, categorized as asynchrony (fewer than 20% of individuals), low synchrony (20–60%), or high synchrony (more than 60%), according to Bencke and Morellato (2002).

Environmental variables

Meteorological data were obtained from the Google Earth Engine platform, a tool for multi-temporal and spatial analysis (Funk *et al.* 2014; 2015), for the same phenological monitoring period. Monthly rainfall data were processed using imagery from the Climate Hazards Group InfraRed Precipitation with Station Data (CHIRPS) satellite, within a defined rectangular polygon that encompassed all study plots. Monthly temperature data were sourced from the ERA5-Land Monthly Averaged - ECMWF Climate Reanalysis (ERA5-LMACR) dataset (Funk *et al.* 2014; Sabater 2021).

Seed germination

A total of 111 seeds were collected from the ground beneath four of the twenty monitored *C. martii* individuals within the study plots for germination testing. After discarding 10 seeds due to damage, the remaining 101 seeds were used in the germination experiment. In the laboratory, the seeds were washed under running water and disinfected with CAPTAN® TS fungicide, following the protocol described by Oliveira *et al.* (2009). The seeds were then distributed into five gerbox containers lined with germitest paper, forming five replicates (four replicates with 20 seeds each and one with 21 seeds).

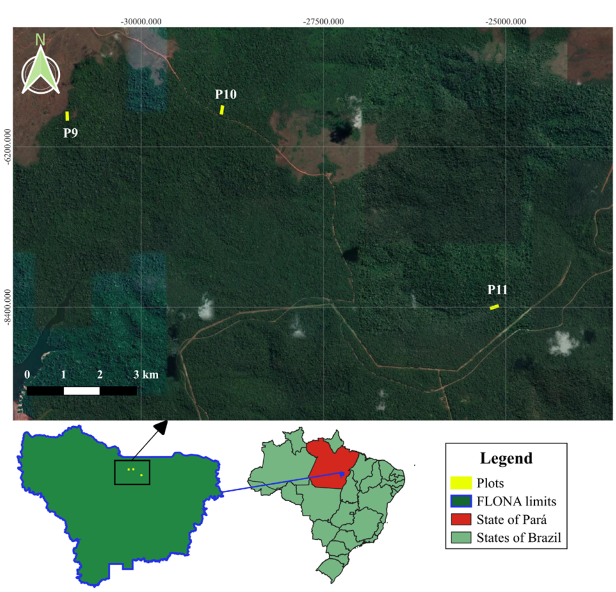

Figure 1. Study plot locations for monitoring *Copaifera martii* in Carajás National Forest, southeastern Pará, Brazil.

The containers were placed in a Biochemical Oxygen Demand (BOD) incubator, following the guidelines of Brasil (2009), under a 12-hour photoperiod at a constant temperature of 20°C. The germination trial was monitored over 115 days, evaluating the germination rate (GR) - defined as the total number of seeds germinated by the end of the evaluation period - as well as the Germination Speed Index (GSI), Mean Germination Time (MGT), and Mean Germination Velocity (MGV) (Maguire 1962; Labouriau and Agudo 1987; Brasil 2009; Amaro 2012).

Data analysis

The seasonality of *Copaifera martii* phenological events was evaluated using circular analysis over the two-year study period (Morellato *et al*. 2010). For the two years of monitoring, the number of *C. martii* individuals exhibiting each phenological event (population activity) per month was converted into angles, with 360° representing the 365 days of the year. The mean angle of occurrence (i.e. the circular mean date) was calculated for each phenophase. This value was interpreted as the most likely period of peak activity for the phenophase and converted into approximate calendar dates for biological interpretation. Subsequently, the Rayleigh test (Brighenti *et al*. 2014) was applied to assess whether the angular data were significantly clustered around a mean direction (Feijoo 2010). This test aimed to determine whether the monitored plants of *C. martii* exhibit significant seasonality (Morellato 2010).

In addition, the mean vector length (*r*) and circular variance were calculated. The mean vector length is a descriptive measure of concentration, ranging from 0 (maximum dispersion) to 1 (perfect alignment), indicating the strength of clustering around a mean direction (Pilon 2015; Barros 2016). In contrast, the Rayleigh test is an inferential approach that evaluates whether the observed clustering significantly deviates from a uniform (random) distribution (Morellato 2010). While both are based on the same underlying circular statistics, they are not redundant: *r* quantifies the degree of directionality, whereas the Rayleigh test assesses its statistical significance (Anastasiadou *et al*. 2019). Thus, we calculated the circular variance, which provides a complementary description of angular dispersion (Brighenti *et al*. 2014).

To assess the relationship between phenophases and climatic seasonality in the Carajás forest, Spearman's correlation analysis (r_s) was conducted at a 5% significance level. The r_s values were interpreted as follows: $|r_s| < 0.20$, negligible correlation; $0.20 \leq |r_s| < 0.40$, weak correlation; $0.40 \leq |r_s| < 0.60$, moderate correlation; $0.60 \leq |r_s| < 0.80$, strong correlation; and $|r_s| > 0.80$, very strong correlation between variables (Brito Neto *et al*. 2018; Leão-Araújo *et al*. 2019). Only climatic variables were considered, as these are typically the main drivers of phenological patterns in tropical species (Opler *et al*. 1976; Reich and Borchert, 1984; Morellato *et al*. 1989). All analyses were performed in R software version 4.4.1, using the circular and plotrix packages (R Core Team 2023).

RESULTS

Climatic factors

There was a relationship between periods of higher temperatures and lower rainfall (June–October), corresponding to the region's dry season, while lower temperatures coincided with increased rainfall, characterizing the rainy season (November–May) (Figure 2).

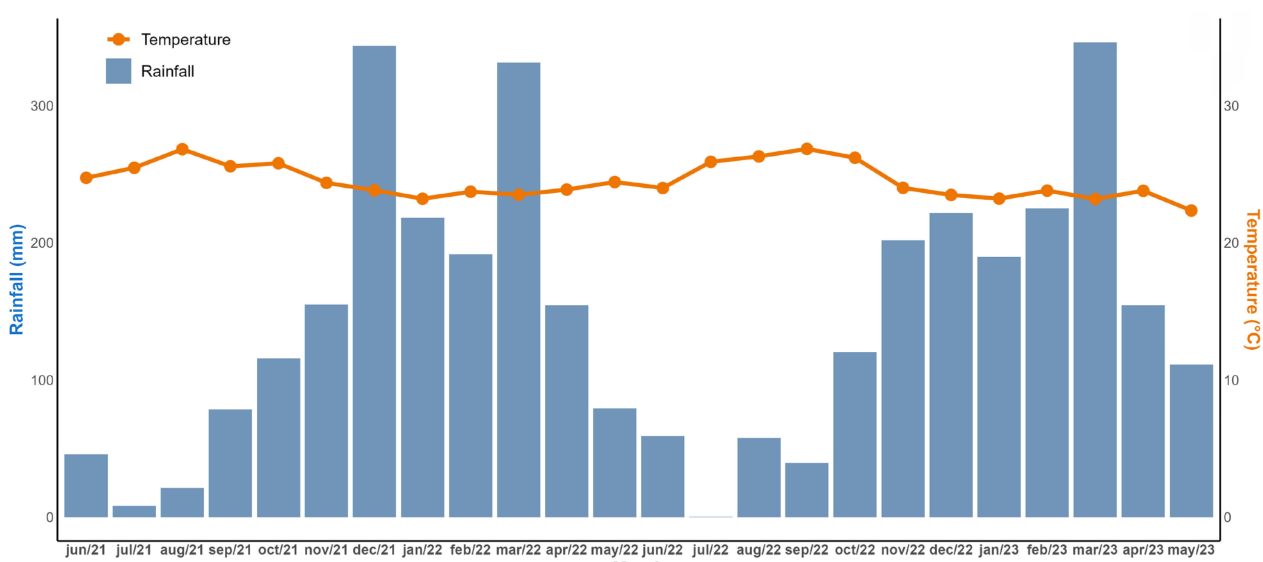

Figure 2. Rainfall and temperature distribution between June 2021 and May 2023 in Carajás National Forest, southeastern Pará, Brazil.

Phenological activity and intensity

The monitored plants of *Copaifera martii* exhibited high synchrony among individuals (≥ 60%) in the emergence of new leaves in September 2021 and August 2022 (Figure 3a). The circular mean angle indicated a peak of new leaves around early September (mean date: September 6, Table 2). Although leaf fall tended to be highly synchronous among individuals, there was no strongly consistent seasonal pattern as for leaf flush (Figure 3b).

Among the months with flowering activity, March 2023 showed the highest synchrony among individuals (both flower buds and flowers in anthesis), while the circular mean angles indicated peak flowering activity around mid-March (mean dates: March 16 for flower buds and March 17 for flowers in anthesis) (Figure 3c, Table 2). High synchrony for fruiting was recorded in July 2021 (ripe fruits, mean date: July 30) and May 2023 (unripe fruits, mean date: May 20), Figure 3e. Although fruits in dispersion did not show high synchrony across the monitoring period (Figure 3e), their mean angle suggested a peak around mid-August (mean date: August 15).

Overall, the phenophases displayed low intensity throughout the monitoring period. Noteworthy events (those with high synchrony, i.e. ≥ 60% of the individuals, see Table 1) included leaf fall between July and August 2021 (Figure 3b), ripe fruits in July 2021 (Figure 3f), the emergence of new leaves in August 2022 (Figure 3b) and flowers in anthesis in March 2023 (Figure 3d). In the remaining months, the phenophases occurred either asynchronously or with low synchrony and intensity.

Phenological seasonality

Seasonality was detected ($p < 0.05$, Table 2) during the monitoring period for the vegetative phenophases of new leaf emergence ($r = 0.39$), and the reproductive phenophases of flower buds ($r = 0.56$), flowers in anthesis ($r = 0.60$), unripe fruits ($r = 0.56$), ripe fruits ($r = 0.70$) and fruit dispersal ($r = 0.57$) (Figure 4).

Spearman's correlation analyses indicated moderate statistical associations between environmental variables and phenological events, such as new leaves and rainfall (r_s = -0.44); flower buds and rainfall (r_s = 0.40); and ripe fruits and rainfall (r_s = -0.51). A moderate correlation was also observed between temperature and unripe fruits (r_s = -0.51) (Table 3). The remaining correlations were either weak or not statistically significant.

Seed germination test

The seed germination test yielded a germination rate of 79.21%, a germination speed index of 3.03 an average germination time of 37.92 days, and a mean germination velocity of 0.03 days^{-1}.

DISCUSSION

This study characterized the phenodynamics of *Copaifera martii* individuals in the Carajás National Forest and evaluated their temporal association with climatic factors over a two-year period (2021–2023). Although the short monitoring period limits definitive conclusions, given that phenological patterns in tropical ecosystems often vary among years and are influenced by multiple environmental drivers, our results suggest that *C. martii* exhibits a seasonal reproductive phenology. Leaf fall occurred throughout the year, peaking during the dry season, while new leaf emergence was concentrated in the transition from the rainy to the dry season. Reproductive events were also seasonal in the scale of the two years of analysis: flowering occurred during the rainy season, fruiting extended through the driest months, and fruit dispersal was concentrated at the end of the dry season. These results provide important ecological insights, offering practical guidance for management and conservation in the eastern Amazon. Moreover, they establish a valuable baseline for future long-term monitoring, which is essential for detecting shifts in phenological patterns, understanding climate–phenology relationships, and predicting species' responses to environmental change.

Leaf fall occurred continuously throughout the year, intensifying during the dry season, while new leaf flushing was concentrated in the rainy-to-dry transition. This pattern is partially consistent with reports for *C. langsdorfii* (Freitas and Oliveira 2002; Pedroni *et al.* 2002) and *C. martii* (Costa and Lameira 2021) yet contrasts with other studies (Almeida *et al.* 2006; Braga *et al.* 2019). The variability among populations is unlikely to be explained solely by differences in rainfall and temperature regimes, which are broadly similar across Amazonian and Cerrado sites. Instead, it likely reflects local heterogeneity in soil fertility, rooting depth, water table dynamics, canopy openness and disturbance history. Such microenvironmental differences can modulate leaf phenology by influencing plant water status, carbon allocation, and susceptibility to herbivores and pathogens (Nomura and Kikuzawa 2003; Janssen *et al.* 2021).

The concentration of leaf flushing in the rainy-to-dry transition may be driven by multiple, non-mutually exclusive mechanisms. Higher soil moisture near the end of the rainy season may promote growth and photosynthetic activation (Longman and Jenik 1987; Wright 1991). Producing mature leaves ahead of the dry season may also improve their stomatal control and limit water loss (Albert *et al.* 2018). Although not experimentally tested here, these mechanisms are consistent with the evergreen strategy (Sarmiento and Monasterio 1983), which maintains a functional canopy year-round. In evergreen tropical forests, continuous litterfall sustains nutrient cycling, replenishes soil organic matter, and supports microbial activity (Sanchez-Galindo *et al.* 2021; Song *et al.* 2023), ultimately influencing forest productivity and resilience.

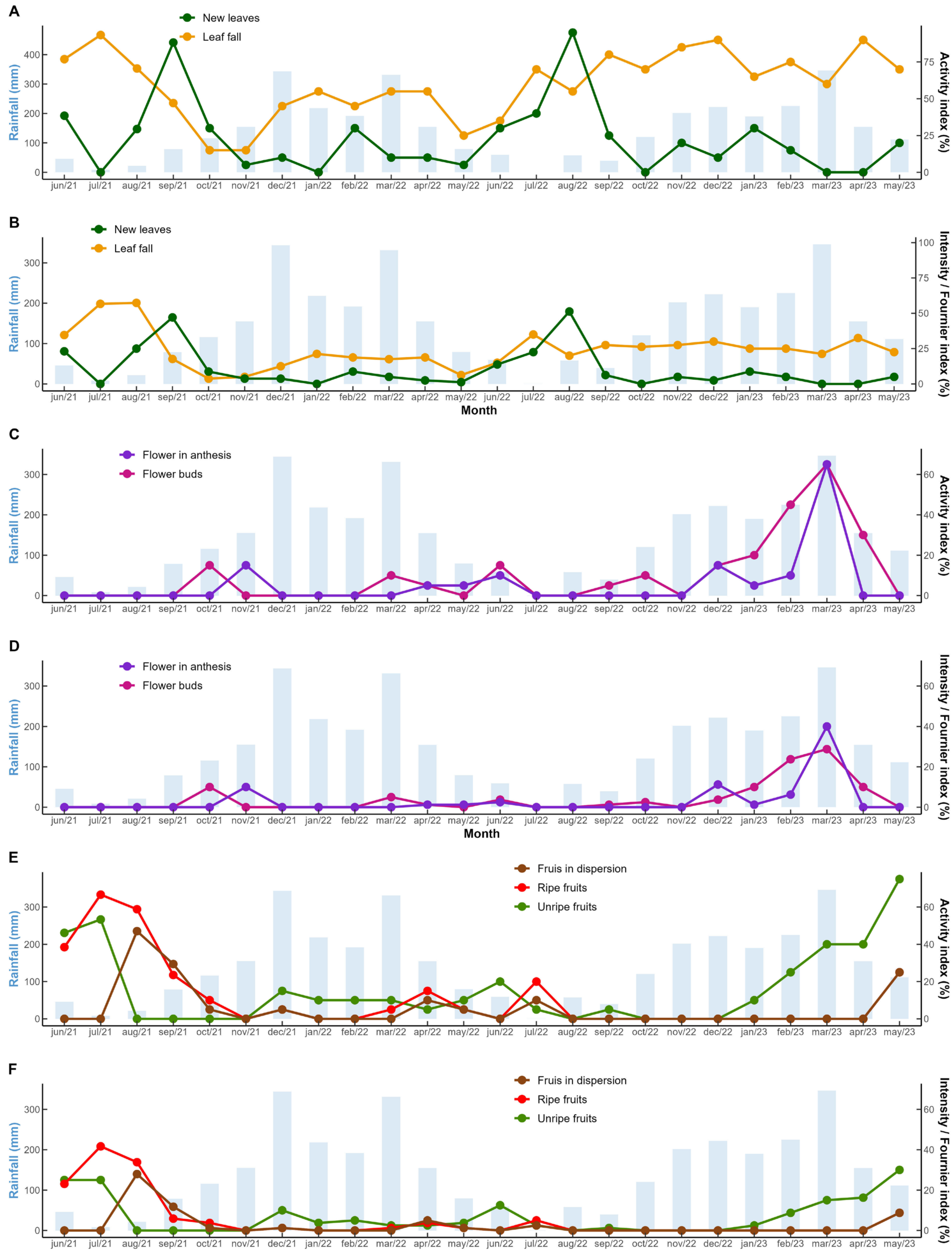

Figure 3. Phenological indices of *Copaifera martii* from June 2021 to May 2023, in the Carajás National Forest, Brazil. Panels (**A**, **C**, **E**) show population activity and (**B**, **D**, **F**) show phenophase intensity, for vegetative phenophases (**A**-**B**), flowering events (**C**-**D**), and fruiting events (**E**-**F**).

Table 1. Percentage of individuals exhibiting each phenophase during months with high activity (synchrony ≥ 60%). Values represent the maximum observed intensity for each phenophase within those months.

Activity (%)		
Phenophase	**Month / Year**	**% of individuals**
Leaf fall	July/2021	93.33
Leaf fall	July/2022	70
Leaf fall	October to March/2023	60 – 90
Leaf fall	April/2023	90
Leaf fall	June/2023	85
New leaves	September/2021	88.24
New leaves	August/2022	95
Flower buds	March/2023	65
Flower in anthesis	March/2023	65
Unripe fruits	May/2021	75
Ripe fruits	July/2021	66.67
Intensity/Fornier (%)		
Phenophase	**Month / Year**	**% of individuals**
Leaf fall	July to August/2022	mean of 51.3
New leaves	August/2022	51.3
Ripe fruits	July/2021	41.7
Flower in anthesis	March/2023	40

Table 2. Results of the Rayleigh test and circular analysis for *Copaifera martii* during the two years of monitoring in Carajás National Forest, southeastern Pará, Brazil. *r:* mean vector; CV: Circular variance. Significant results are highlighted in bold.

Phenophase	Mean angle	Mean date	*r*	CV	Rayleigh (Z)	p-value
Leaf fall	165.91	16/June	0.030	0.969	0.030	0.257
New leaves	246.02	06/September	0.392	0.607	0.393	**< 0.05**
Flower buds	73.73	16/March	0.562	0.437	0.563	**< 0.05**
Flower in anthesis	74.81	17/March	0.601	0.398	0.601	**< 0.05**
Unripe fruits	139.70	20/May	0.562	0.437	0.562	**< 0.05**
Ripe fruits	209.54	30/July	0.700	0.299	0.700	**< 0.05**
Fruits in dispersion	224.86	15/August	0.577	0.423	0.577	**< 0.05**

Flowering in *C. martii* occurred predominantly during the rainy season, contrasting with the common dry-season flowering in many tropical tree species (Maués 2002; Parolin *et al*. 2011; Dantas *et al*. 2021). This pattern, also reported for *certain C. langsdorfii* populations (Dias and Oliveira 1996; Almeida *et al*. 2006), suggests that high humidity may enhance pollen viability, stigma receptivity, and early fruit development. Despite the divergence in flowering seasonality, dispersal still occurred at the end of the dry season, synchronizing seed release with the onset of rains and maximizing germination potential (Borchert *et al*. 2004). The marked increase in floral activity during the drier second year indicates reproductive sensitivity to interannual climatic variation, though longer time series are required to determine whether such differences represent cyclical responses or stochastic fluctuations.

Fruiting was concentrated in the dry season, with dispersal peaking just before the first rains, a sequence widely documented among tropical trees (Gouveia and Felfili 1998; Vieira *et al*. 2008). This timing allows for physiological maturation under low humidity, promotes fruit dehiscence (Gautier-Hion 1990; Da Silva 2018), and ensures that seeds encounter favorable soil moisture for germination (Garwood 1983; Escobar *et al*. 2018; Martins *et al*. 2019). While zoochory is predominant in *Copaifera* (Carvalho 2003), our observations of numerous seeds beneath parent trees suggest that barochory or other abiotic mechanisms may play a complementary role. These mixed dispersal strategies could influence seed shadow patterns, seedling establishment, and genetic structure within populations, with potential implications for regeneration dynamics in both intact and disturbed habitats.

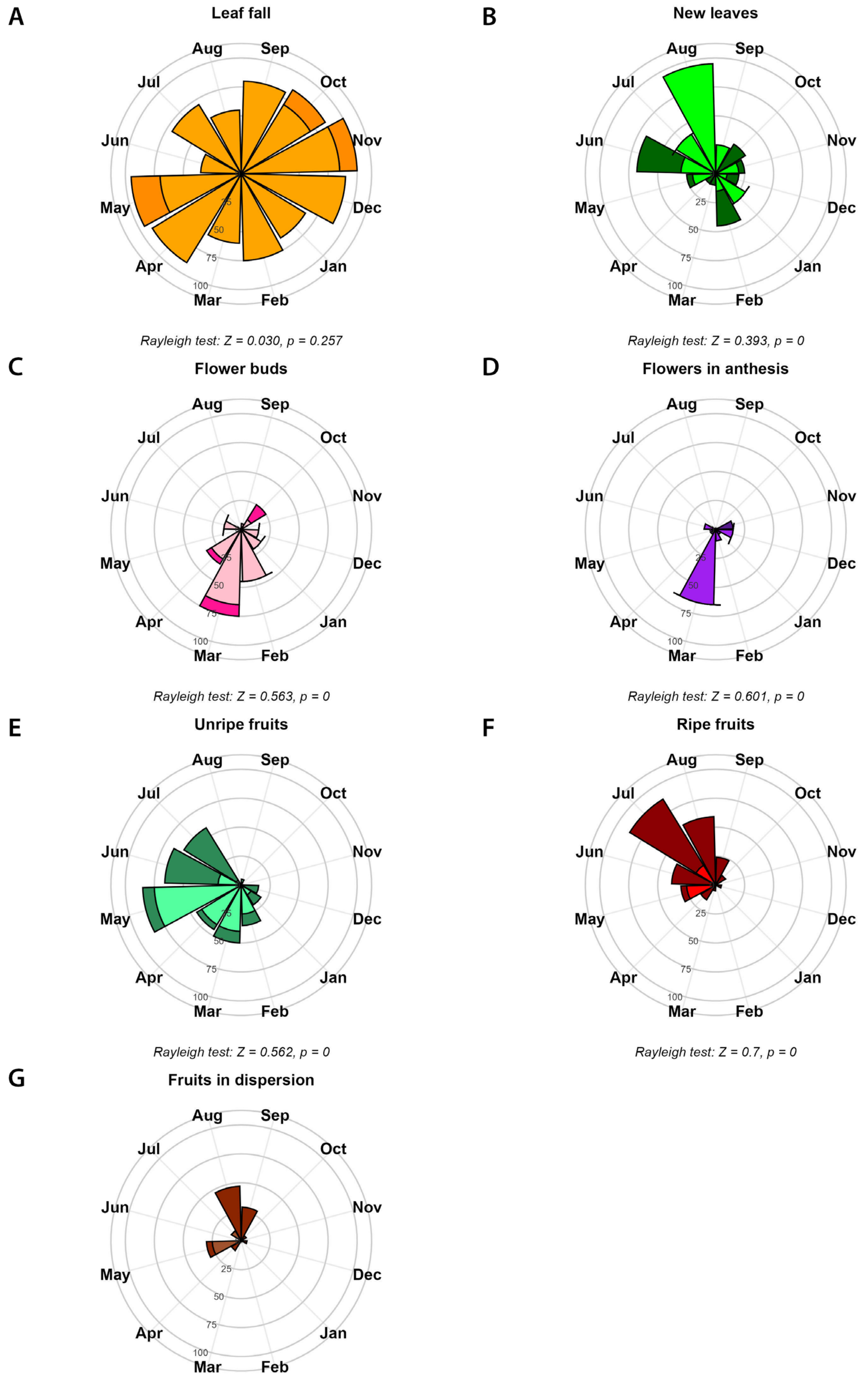

Figure 4. Population activity of the phenophases of *Copaifera martii* from June 2021 to May 2023, in Carajás National Forest, Brazil. Phenophases include: (**A**) leaf fall, (**B**) new leaves, (**C**) flower buds, (**D**) flowers in anthesis, (**E**) unripe fruits, (**F**) ripe fruits and (**G**) fruits in dispersion. Darker shades represent the first year of monitoring, while lighter shades correspond to the second year.

Table 3. Spearman's correlation analysis (r_s) between the evaluated phenophases: leaf fall (LF), new leaves (NL), flower buds (FB), flowers in anthesis (FA), unripe fruits (UF), ripe fruits (RF) and fruits in dispersion (FD) of *Copaifera martii* and climatic factors (monthly precipitation and temperature) in the Carajás National Forest. Bolded r_s values are marked with "*" to indicate a significant (<0.05) and moderate correlation.

Phenophase Climatic factor	LF	NL	FB	FA	UF	RF	FD
Rainfall (mm)	-0.163	**-0.436***	**0.405***	0.382	0.081	**-0.513***	-0.325
Temperature (°C)	0.024	0.364	-0.327	-0.379	**-0.510***	0.278	0.229

Leaf flushing tended to intensify as rainfall declined, possibly allowing leaves to mature before the peak of the dry season, optimizing water-use efficiency (Pessoa 2014; Janssen *et al*. 2021). Additionally, synchronizing leaf flushing with periods of declining rainfall could potentially reduce pressure from herbivores and microbial pathogens, which tend to be more active during wetter periods (Lopes *et al*. 2016). Mean temperature was associated with the formation of immature reproductive organs, suggesting that even modest thermal variation in the Amazon can serve as an additional cue for transitions between reproductive stages. Similar relationships have been observed in other tropical systems (Longo *et al*. 2018; Santos *et al*. 2022), supporting the hypothesis that *C. martii* phenology is influenced by a combination of seasonal climatic cues and endogenous controls. Nonetheless, due to the limited temporal scope of the study, these associations should be interpreted as indicative rather than causal, underscoring the importance of long-term monitoring to disentangle climatic from intrinsic drivers.

Germination tests revealed high viability (79.2%) and a germination speed index of 3.03 without the need for dormancy-breaking treatments, contrasting with many *Copaifera* species that exhibit physical or physiological dormancy (Amaro 2012; Nascimento *et al*. 2021). The mean germination time of 37 days reinforces the absence of dormancy and suggests a regeneration strategy geared toward rapid recruitment after dispersal. This trait is advantageous in colonizing canopy gaps and disturbed sites, particularly under scenarios of increased disturbance frequency associated with climate change. From a management perspective, the absence of dormancy reduces the costs of seedling production, facilitating ecological restoration and supporting community-based seed supply chains.

CONCLUSIONS

While the two-year scope of this study limits mechanistic interpretation, it provides a baseline for future long-term (>10 years) monitoring, which is essential for capturing the full range of temporal variability and anticipating responses to climate change (Aleixo 2019). Our findings already offer direct applications for sustainable management, including defining optimal seed collection periods, informing harvest quotas, and guiding restoration planning. Integrating phenological data with adaptive management strategies will be key to ensuring the resilience of both natural populations and the socio-ecological systems that depend on them in one of the Amazon's most ecologically and economically significant regions.

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REFERENCES

Albert, L.P.; Wu, J.; Prohaska, N.; de Camargo, P.B.; Huxman, T.E.; Tribuzy, E.S.; *et al*. 2018. Age-dependent leaf physiology and consequences for crown-scale carbon uptake during the dry season in an Amazon evergreen forest. *New Phytologist*, 219: 870–884.

Aleixo, I.F. 2019. Padrões fenológicos e mortalidade de árvores de terra firme na Amazônia Central. Doctoral thesis. Instituto Nacional de Pesquisas da Amazônia. 201 p. (https://repositorio.inpa.gov.br/items/e1c11aee-9f74-4994-aca7-5226af20dd57).

Almeida, C.I.M.; Leite, G.L.D.; Rocha, S.L.; Machado, M.M.L.; Maldonado, W.C.H. 2006. Fenologia e artrópodes de *Copaifera langsdorffii* Desf. no Cerrado. *Revista Brasileira de Plantas Medicinais,* 8: 64-70.

Alvares, C.A.; Stape J.L.; Sentelhas, P.C.; Gonçalves, J.L.M.; Sparovek, G. 2013. Mapa de classificação climática de Köppen para o Brasil. *Meteorologische Zeitschrift*, 22: 711-728.

Amaro, M.S. 2012. Germinação de sementes e mobilização de reservas em plantas de copaíba sob estresses hídrico e salino. Doctoral thesis. Universidade Federal do Ceará, Brazil, 135 p. (https://repositorio.ufc.br/handle/riufc/8631)

Anastasiadou, M.N.; Christodoulakis, M.; Papathanasiou, E.S.; Papacostas, S.S.; Hadjipapas, A.; Mitsis, G.D. 2019. Graph theoretical characteristics of EEG-based functional brain networks in patients with epilepsy: the effect of reference choice and volume conduction. *Frontiers in Neuroscience,* 13: 1-18.

Barros, A.J.L.S. 2016. Contributo da estatística circular no estudo (direção e inclinação) de planos e estruturas geológicas. Master's dissertation. Faculdade de Engenharia Universidade do Porto, Portugal, 134p. (https://oasisbr.ibict.br/vufind/Record/RCAP_9a1793cf83a5a708236d2e86e98a8339)

Belo, R.M.; Negreiros, D.; Fernandes, G.W.; Silveira, F.A.O.; Ranieri, B.D.; Morellato, P.C. 2013. Fenologia reprodutiva e vegetativa de arbustos endêmicos de campo rupestre na Serra do Cipó, Sudeste do Brasil. *Rodriguésia,* 64: 817-828.

Bencke, C.S.C.; Morellato, L.P.C. 2002. Comparação de dois métodos de avaliação da fenologia de plantas, sua interpretação e representação. *Revista Brasileira de Botânica,* 25: 269-275.

Bessa, A.F.V.; Donadon, J.R.; Resende, O.; Alves, R.M.V.; Sales, J.F.; Costa, L.M. 2015. Armazenamento do crambe em diferentes embalagens e ambientes: Parte I - Qualidade fisiológica. *Revista Brasileira de Engenharia Agrícola e Ambiental,* 19: 231– 237.

Borchert, R.; Meyer, S.; Felger R.S.; Bolland L.P. 2004. Environmental control of flowering periodicity in Costa Rican and Mexican tropical dry forests. *Global Ecology and Biogeography,* 13: 409-425.

Braga, A.M.S.; Lima, G.A.; Teodoro, M.S.; Lemos, J.R. 2019. Fenologia de três espécies arbóreas em um trecho de vegetação subcaducifólia no norte do Piauí, Brasil. *Biotemas,* 32: 33-44.

Brasil. 2009. Ministério da Agricultura, Pecuária e Abastecimento - MAPA. Regras para análise de sementes. (https://www.gov.br/agricultura/pt-br/assuntos/insumos-agropecuarios/arquivos-publicacoes-insumos/2946_regras_analise__sementes.pdf). Accessed on 13 Feb 2025.

Brighenti, C. R. G.; Brighenti, D. M.; Miranda, Y. S. S.; Oliveira, T. G. S. 2014. Von mises distribution in the evaluation of apicultural data. *Archivos de Zootecnia,* 63: 461-471

Brito Neto, R.L.; Araújo, E.I.P.; Maciel, C.M.S.; Paula, A.; Tagliaferre, C. 2018. Fenologia de *Astronium graveolens* Jacq. em floresta estacional decidual em Vitória da Conquista, Bahia. *Ciência Florestal,* 28: 641-650.

Buisson, E.; Swanni, T.A.; Le Stradic, S.; Morellato, L.P.C. 2017. Plant phenological research enhances ecological restoration. *Restoration Ecology*, 25: 164-171.

Calvi, G.P.; Piña-Rodrigues, F.C.M. 2016. Fenologia e produção de sementes de *Euterpe edulis*-Mart em trecho de floresta de altitude no Município de Miguel Pereira-RJ. *Revista Universidade Rural: Série Ciências da Vida,* 25: 33-40.

Carvalho, P.E.R. 2003. Espécies arbóreas brasileiras, Vol.1. Brasília: Embrapa Informação Tecnológica. 1039p.

Cattanio, J.H.; Anderson, A.B.; Rombold, J.S.; Nepstad, D.C. 2004. Phenology, litterfall, growth, and root biomass in a tidal floodplain forest in the Amazon estuary. *Brazillian Journal of Botany,* 4: 703-712.

Colado, M.L.Z.; Reis, L.K.; Guerra, A.; Ferreira, B.H.S.; Fonseca, D.R.; Timóteo, A.; *et al.* Key decision-making criteria for dormancy-breaking and ability to form seed banks of Cerrado native tree species. *Acta Botanica Brasilica,* 34: 694-703

Costa, A.C.G.; Vasconcelos, L.V.; Lima, C.T.; Caldeira, C.F.; Zappi, D.C.; Giulietti, A.M. *et al.* 2023. Reproductive phenology of critical native plant species for mineland restoration in the eastern Amazon. *Plant Species Biology,* 38: 131-143

Costa, A.S.; Lameira, O.A. 2021. Avaliação do comportamento fenológico da *Copaifera martii* (Hayne) com dados climáticos em Floresta Secundária. *Research, Society and Development,* 10: 1-22.

Cruz, E.D.; Kato, O.R.; Gurgel, E.S.C. 2022. Germinação de sementes de espécies amazônicas: copaíba-jutaí (*Copaifera martii* Hayne). *Comunicado técnico Embrapa nº 355*. (https://www.infoteca.cnptia.embrapa.br/infoteca/handle/doc/1150026?mode=full).

Dantas A.R.; Guedes, M.C.; Lira-Guedes, A.C.; Piedade, M.T.F. 2021. Phenological behavior and floral visitors of *Pentaclethra macroloba* a hyperdominant tree in the Brazilian Amazon River estuary. *Trees,* 35: 973-986

Da Silva, P.O. 2018. Fenologia reprodutiva de *Hymenaea stigonocarpa* Mart ex Hayne (Fabaceae) em cerrado sensu stricto. *Acta Biológica Catarinense,* 5: 89-97.

Dias, H.C.T.; Oliveira-Filho, A.T. 1996. Fenologia de quatro espécies arbóreas de uma floresta estacional semidecídua montana em Lavras, MG. *Cerne*, 2: 66-88.

Escobar, D.F.E.; Silveira, F.A.O.; Morellato, L.P.C. 2018. Timing of seed dispersal and seed dormancy in Brazilian savanna: two solutions to face seasonality. *Annals of Botany,* 121: 1197-1209.

Fearnside, P. 1989. The charcoal of Carajas: a threat to the forests of Brazil's eastern Amazon region. *Ambio,* 18: 141-143

Feijoo, A.M.L.C. 2010. *A pesquisa e a estatística na psicologia e na educação*. Centro Edelstein de Pesquisas Sociais, Rio de Janeiro. 272p.

Ferreira, B.H.S.; Freitas, T.G.; Arakaki, L.M.M.; Covre, W.S.; Damasceno-Junior, G.A.; Galleto, L.; *et al.* 2024 Vegetative and reproductive phenology in seasonal climate vegetation: phenological complementarity between woody and herbaceous plants in the Brazilian Chaco. *Flora,* 316:1-11

Ferreira, L.C.O.; Fernandes, G.G.C.; Vieira, A.L.M.; Albuquerque, A.R. 2022. Produtos Florestais não Madeireiros do Brasil (2016-2020): Subsídio ao Estabelecimento de Novas Cadeias Produtivas pela Cooperativa de Extrativistas de Carajás. *Biodiversidade Brasileira Bio Brasil,* 12: 220-232.

Fournier, L.A. 1974. Un método cuantitativo para la medición de características fenológicas en árbores. *Turrialba,* 24: 422-423.

Freitas, C.V.; Oliveira, P.E. 2002. Biologia reprodutiva de *Copaifera langsdorffii* Desf. (Leguminosae, Caesalpinioideae. *Brazilian Journal of Botany,* 25: 311- 321.

Funk, C.C.; Peterson, P.J.; Landsfeld, M.F.; Pedreros, D.H.; Verdin, J.P.; Rowland, J.D; *et al.* 2014. A quasi-global precipitation time series for drought monitoring. *US Geological Survey Data Series,* 832: 1-12.

Funk, C.C.; Peterson, P.J.; Landsfeld, M.F.; Pedreros, D.H.; Verdin, J.P.; Shukla, S.; *et al.* 2015. The climate hazards infrared precipitation with stations - a new environmental record for monitoring extremes. *Scientific Data,* 02: 150066.

Garwood, N.C. 1983. Seed Germination in a Seasonal Tropical Forest in Panama: A Community Study. *Ecological Monographs,* 53: 159–181.

Gautier-Hion, A. 1990. Interactions among fruit and vertebrate fruit-eaters in an African tropical rain forest. In: Bawa, K.S.; Hadley, M. (Eds.). *Reproductive ecology of tropical forest plants - Man and the Biosphere Series*. The Parthenon Publishing Group, Paris. 7: 219-230.

Girardin, C.A.; Malhi, Y.; Doughty, D.B.M.; Meir, P.; Aguila-Pasquel, J.; Araujo-Murakami, A. *et al.* 2016. Seasonal trends of Amazonian rainforest phenology, net primary productivity, and carbon allocation. *Global Biogeochemical Cycles,* 30: 700-715.

Gouveia, G.P.; Felfili, J.M. 1998. Fenologia de comunidades de cerrado e de mata de galeria no Brasil Central. *Revista Árvore,* 22: 443-450.

Hilker, T.; Lyapustin, A.I.; Tucker, C.J.; Hall, F.G.; Myneni, R.B.; Wang, Y.; Bi, J.; *et al.* 2014. Vegetation dynamics and rainfall sensitivity of the Amazon. *Proceedings of the National Academy of Sciences of the United States of America*, 111: 16041-16046.

ICMBIO. 2017. Plano de pesquisa de geossistemas ferruginosos da Floresta Nacional de Carajás, Brasília. (https://www.gov.br/icmbio/pt-br/assuntos/biodiversidade/unidade-de-conservacao/unidades-de-biomas/amazonia/lista-de-ucs/flona-de-carajas/arquivos/plano_de_pesquisa_flona_carajas_-_06-09-2017_-_final_2.pdf). Accessed on 13 Feb 2025.

Janssen, T.; van der Velde, Y. ; Hofhansl, F.; Luyssaert, S.; Naudts, K.; Driessen, B. ; *et al.* 2021. Drought effects on leaf fall, leaf flushing and stem growth in the Amazon forest: reconciling remote sensing data and field observations. *Bioeosciences,* 18: 4445-4472.

Labouriau, L.G.; Agudo, M. 1987. On the physiology of seed germination in *Salvia hispanica* L.I. Temperature effects. *Anais da Academia Brasileira de Ciências,* 59: 37-56.

Leão-Araújo, E.F.; De Souza, E.R.B.; Naves, R.V.; Peixoto, N. 2019. Phenology of *Campomanesia adamantium* (Cambess.) O. Berg in Brazilian Cerrado. *Revista Brasileira de Fruticultura,* 41: 1-12.

Lenza, E.; Klink, C.A. 2006. Comportamento fenológico de espécies lenhosas em um cerrado sentido restrito de Brasília, DF. *Brazilian Journal of Botany,* 29: 627-638

Longman, K.A.; Jenik, J. 1987. Tropical forest and its enviroments. 2nd ed. Longman Scientific & Technical, Harlow, Essex. 347p.

Longo, M.; Knox, R.G.; Levine, N.M.; Alves, L.F.; Bonal, D.; Camargo, P.B.; *et al.* 2018. Ecosystem heterogeneity and diversity mitigate Amazon forest resilience to frequent extreme droughts. *New Phytologist,* 219: 914-931.

Lopes, A.P.; Nelson, B.W.; Wu, J.; Graça, P.M.L.A.; Tavares, J.V.; Prohaska, N.; *et al.* 2016. Leaf flush drives dry season green-up of the Central Amazon. *Remote Sensing of Environment,* 182: 90-98.

Maguire, J.D. 1962. Speed of Germination—Aid In Selection and Evaluation for Seedling Emergence and Vigor. *Crop Science* 2: 176-177.

Martins, A.A.; Øystein, H.O.; William, S.A.; Pélabon, C. 2019. Rainfall seasonality predicts the germination behavior of a tropical dry-forest vine. *Ecology and Evolution,* 9: 5196-5205.

Martins, W.A.; Santos, S.C.; Jara, R.S.; Souza, J.L.A.C.; Galvão, J.R.; Biscaro, G.A. 2019. Fenologia e demanda térmica de amoreira-preta cv. Tupy. *Revista de Ciências Agrárias,* 42: 720-730.

Maués, M.M. 2002. Reproductive phenology and pollination of the Brazil nut tree (*Bertholletia excelsa* Humb. & Bonpl. Lecythidaceae) in Eastern Amazonia. *Agricultural and Food Sciences, Environmental Science,* 245: 1-10

Morellato, L.P.C.; Talora, D.C.; Takahasi, A.; Bencke, C.S.C.; Romera, E.C.; Zipparro, V. 2000. Phenology of Atlantic rain forest trees: a comparative study. *Biotropica*. 32: 811-823.

Morellato, L.P.C.; Alberti, L.F; Hudson, I.L. 2010. Applications of Circular Statistics in Plant Phenology: a Case Studies Approach. In: Keatley, M.R. (Ed.). *Phenological research*. New York, Springer. p.339-359.

Morellato, L.P.C.; Alberton, B.; Swanni, T.A.; Borges, B.; Buisson, E.; Camargo, M.G.G.; *et al.* 2016. Linking plant phenology to conservation biology. *Biological Conservation* 195: 60-72.

Morellato, L.P.C.; Rodrigues, R.R.; Leitão-Filho, H.F.; Joly, C.A. 1989. Estudo comparativo da fenologia de espécies arbóreas de floresta de altitude e floresta mesófila semidecídua na Serra do Japi, Jundiaí, São Paulo. *Revista Brasileira de Botânica* 12: 85-98.

Morellato, L.P.C. 1992. *História natural da Serra do Japi: ecologia e preservação de uma área florestal no Sudeste do Brasil*. Editora UNICAMP, Campinas. 110p.

Muñoz-Sabater, J.; Dutra, E.; Agustí-Panareda, A.; Albergel, C.; Arduini, G.; Balsamo, G.; *et al.* 2021. ERA5-Land: A state-of-the-art global reanalysis dataset for land applications. *Earth System Science Data* 13: 4349–4383

Nascimento, E.V.; Bonilla, O.H.; Lucena, E.M.P.; Filho, J.V.R.; Pinheiro, H.B.; Nascimento, Y.A.P.; Lima, F.R.A. 2021. Superação de dormência em sementes de *Copaifera duckei* Dwyer. (Fabaceae). *Brazilian Journal of Development* 7: 33338-33356.

Nogueira, D.A.R.; Jaerger, S.; Fin, M.T.; Mainarders, R.M.; Zatta, L.; Tormen, L.; *et al.* 2022. Liberação lenta do óleo de copaíba adsolubilizado em hidróxidos duplos lamelares: um material promissor para pomadas cutâneas. *Química Nova* 54: 921-928.

Nomura, N.; Kikuzawa, K. 2003. Productive phenology of tropical montane forests: Fertilization experiments along a moisture gradient. *Ecological Research* 18: 573–586.

Oliveira, M.D.M.; Nascimento, L.C.; Alves, E.U.; Gonçalves, E.P.; Guedes, R.S. 2009. Tratamentos térmico e químico em sementes de mulungu e efeitos sobre a qualidade sanitária e fisiológica. *Revista Caatinga* 22: 150-155.

Opler, P.A.; Frankie, G.W.; Baker, H.G. 1976. Precipitação como um fator na liberação, tempo e sincronização da antese por árvores e arbustos tropicais. *Jornal de Biogeografia* 3: 231-236.

Parolin, P.; Wittmann, F. 2011. Tree Phenology in Amazonian Floodplain Forests. In: Schöngart, J. (Ed.). *Amazonian Floodplain Forests:* Ecophysiology, *Biodiversity and Sustainable Management*. Springer, Dordrecht. p.105-126.

Pau S.; Wolkovich, E.M.; Cook, B.I.; Nytch, C.J.; Regetz, J.; Zimmerman, J.K. *et al.* 2013. Clouds and temperature drive dynamic changes in tropical flower production. *Nature Climate Change,* 3: 838-842.

Pedroni, F.; Sanchez, M.; Santos, F.A.M. 2002. Fenologia da copaíba (*Copaifera langsdorffii* Desf. -- Leguminosae, Caesalpinioideae) em uma floresta semidecídua no sudeste do Brasil. *Revista Brasileira de Botânica,* 25: 183-194

Pedrozo, E.A.; Silva, T.N.; Sato, S.A.S.; Oliveira, N.D.A. 2017. Produtos Florestais Não Madeiráveis (PFNMs): as filières do açaí e da castanha da Amazônia. *Revista de Administração e Negócios da Amazônia* 3: 88-112.

Pessoa, A.C.B.P. 2014. Influência da sazonalidade nos mecanismos de fotossíntese e fotoproteção em plantas adultas de *Poincianella pyramidalis* (Tul.) L. P. Queiroz (Catingueira). Master's dissertation. Universidade Federal de Pernambuco, Brazil, 70p.

Pilon, N.A.L.; Udulutsch, R.G.; Durigan, G. 2015. Padrões fenológicos de 111 espécies de Cerrado em condições de cultivo. *Hoehnea* 42: 425-443.

Pinheiro, J.C.; Gama, J.R.V.; Oliveira, F.A.; Ribeiro, R.B.S.; Cruz, G.S. 2019. Fitossociologia e expectativa de renda com produtos florestais madeireiros e não madeireiros em assentamento no Pará. *Nativa* 7: 101-108.

Primack, R.B. 1987. Relationships among flowers, fruits, and seeds. *Annual Review of Ecology and Systematics* 18: 409-430.

R Core Team (2023). *R: A Language and Environment for Statistical Computing* (Version 4.4.1). R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reich, P.B.; Borchert, R. 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology* 72: 61-74.

Rosa, J.C.; Gomes, A.M.S. 2009. Os aspectos etnobotânicos da copaíba. *Revista Geografar* 4: 59-77.

Rosseto, J.; Albuquerque, M.C.F.; Neto, R.M.R.; Silva, I.C.O. 2009. Germinação de sementes de *Parkia pendula* (Willd.) Benth. ex Walp. (Fabaceae) em diferentes temperaturas. *Revista Árvore* 33: 47-55.

Sanchez-Galindo, L.M.; Sandmann, D.; Marian, F.; Krashevska, V.; Maraun, M.; Scheu, S. 2021. Leaf litter identity rather than diversity shapes microbial functions and microarthropod abundance in tropical montane rainforests. *Ecology and Evolution* 11: 2360-2374.

Santana, A.S.; Giacobbo, C.L.; Prado, J.; Uberti, A.; Louis, B.; Alberto, C.A. 2020. Fenologia e qualidade de frutos de acessos de *Physalis* spp. *Revista Agrarian* 13: 1-8.

Santos, J.L.R. 2018. Território em transe: a Floresta Nacional de Carajás. *Anais from the V Encontro Nacional da Associação Nacional de Pós-Graduação e Pesquisa em Ambiente e Sociedade (ANPPAS)* 7: 1-11.

Santos, M.O.; Almeida, B.V.; Campos, N.B.; Macedo, J.G.F.; Macêdo, M.J.F.; Ribeiro, D.A.; *et al*. 2022. Vegetative and reproductive phenology of *Copaifera langsdorffii* Desf. in different phytophysiognomies. *Research, Society and Development* 11: 1-27.

Sarmiento, G.; Monasterio, M. 1983. Formas de vida e fenologia. *Ecossistemas do Mundo* 13: 79-108.

Scatigna, A.V.; Oliveira, N.F.; Viana, P.L. 2017. *Buchnera carajasensis* (Orobanchaceae), a new species from the canga vegetation of the Serra dos Carajás, Pará, Brazil. *Kew Bulletin* 72: 1-8.

Segrestin, J.; Bernard-Verdier, M.; Violle, C.; Richardte, J.; Navas, M.; Garnier, E. 2018. When is the best time to flower and disperse? A comparative analysis of plant reproductive phenology in the Mediterranean. *Functional Ecology* 32: 1770-1783.

Sidião, W.B.; Mendes, D.B.; Oliveira, L.R.; Barboza, F.S.; Coneglian, A. 2018. A Superação de dormência em sementes de Copaíba submetidas a escarificação mecânica. *Anais da Semana de Ciências Agrárias da Pós-Graduação em Produção Vegetal* 15: 227-230.

Silva, J.O.; Espírito-Santo, M.M.; Santos, J.C.; Rodrigues, P.M.S. 2020. Does leaf flushing in the dry season affect leaf traits and herbivory in a tropical dry forest? *Science of Nature,* 107: 1–10.

Song Y.; Yu, Y.; Li, Y.; Mu, M. 2023. Leaf litter chemistry and its effects on soil microorganisms in different ages of *Zanthoxylum planispinum* var. *Dintanensis*. *BMC Plant Biology* 23: 1-14.

Sonter, L. J.; Herrera, D.; Barrett, D. J.; Galford, G. L.; Moran, C. J.; & Soares-Filho, B. S. (2017). Mining drives extensive deforestation in the Brazilian Amazon. *Nature Communications*, 8: 1–7.

Stevaux, R.S.; Alves, A.F. 2022. Subsídios ao uso de *Copaifera langsdorffii* Desf. para produção de óleo. *Revista Brasileira de Agroecologia* 17: 322-338.

Tannus, J.L.S.; Assis, M.A.; Morellato, L.P.C. 2006. Fenologia reprodutiva em campo sujo e campo úmido numa área de Cerrado no sudeste do Brasil, Itirapina – SP. *Biota Neotropica* 6: 10-27.

Torres, M.F.O.; Dantas, S.J.; Souza, J.L.; Nunes, V.V.; Calazans, C.C.; Ferreira, O.J.M.; Mann, R.S.; Ferreira, R.A. 2020. Curva de embebição e viabilidade de sementes de *Sapindus saponaria* L. *Global Science and Technology* 13: 211-218.

Vasconcelos, R.G.; Linhares, A.C.C.; Marques, M.B.L.; Alves, S.R.M. 2020. Análise da oferta de oleorresina de copaíba (*Copaifera* spp.) no Brasil e do dinamismo do valor da produção. *Diversistas Journal* 5: 684-692.

Vieira, D.L.M.; Lima, V.V.; Sevilha, A.C.; Scariot, A. 2008. Consequences of dry-season seed dispersal on seedling establishment of dry forest trees: Should we store seeds until the rains? *Forest Ecology and Management* 256: 471–481.

Wikander, T. 1984. Mecanismos de dispersión de diasporas de una selva decidua en Venezuela. *Biotropica* 16: 276- 283.

Wright, S.J. 1991. Seasonal drought and the phenology of understory shrubs in a tropical moist forest. *Ecology* 72: 1643-1657.

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