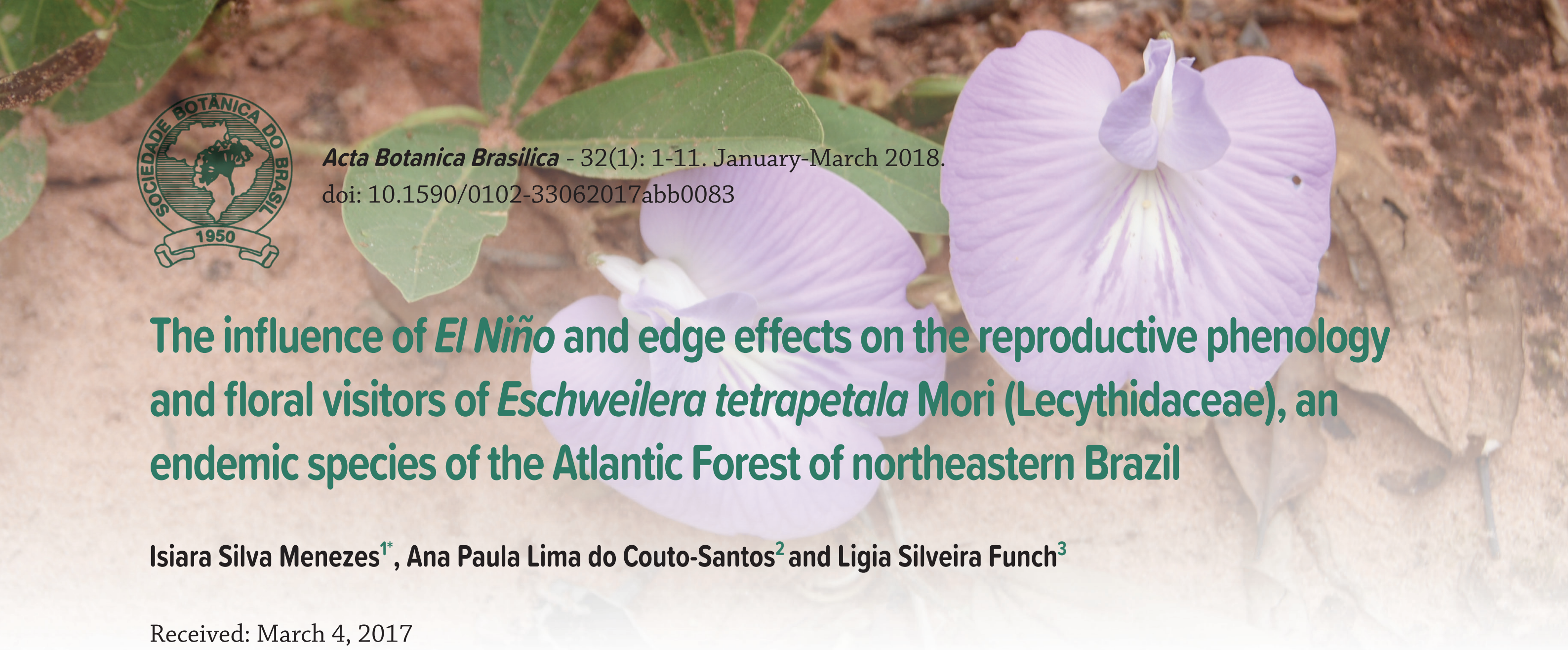

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The influence of *El Niño* and edge effects on the reproductive phenology and floral visitors of *Eschweilera tetrapetala* Mori (Lecythidaceae), an endemic species of the Atlantic Forest of northeastern Brazil

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ABSTRACT

We compared the reproductive phenology and floral visitors of *Eschweilera tetrapetala* growing along the edge and in the interior of a submontane forest in the Chapada Diamantina mountains, Bahia State, Brazil. We sought to determine if there were inter-annual differences in intensity and seasonality associated with environmental conditions, and if there were differences in floral visitors between the two environmental contexts. Phenological observations were performed for three years, and included the occurrence of an *El Niño* event. We applied circular statistics to detect seasonal trends, performed cross correlations between phenophases and climate, Kruskal-Wallis and Wilcoxon signed-rank tests for inter-annual variation, and the Wilcoxon-Mann-Whitney test for edge-interior differences in the species richness of floral visitors. We observed inter-annual variations in the intensity and seasonality of flower production that accompanied variations in rainfall, possibly associated with *El Niño* events. Floral visitor richness differed between the forest edge and interior, with seven species recorded for the interior and only one for the edge. Reduced fruit set was also observed at the forest edge. This study contributes to our understanding of the influence of *El Niño* and edge effects on the reproductive phenologies of tropical plants.

Keywords: *El Niño*, *Eschweilera tetrapetala*, floral visitors, linear edge effects, phenology, precipitation, seasonality

Introduction

Climate change, fragmentation, and loss of natural areas are among the principal global threats to biodiversity (Klapwijk & Lewis 2008). There is indisputable evidence that edge effects resulting from forest fragmentation can modify the richness and abundance of tropical arboreal species (e.g., Oliveira *et al.* 2004; Pires *et al.* 2014; Couto-Santos *et al.* 2015). The phenology and reproductive success of plant species occurring near forest edges can be strongly affected by their different environmental conditions (Aguilar & Galleto 2004; Athayde & Morellato 2014). Reductions in the availability of abiotic resources such as water and soil nutrients in edge environments, for example, can limit the fruiting rates of the plants there as compared to those growing in the forest interior (Dunley *et al.* 2009; Athayde & Morellato 2014).

Disturbances of plant-pollinator interactions can also result from habitat fragmentation, and edge effects can further alter pollinator frequencies and abundances - and therefore pollination services - which can lead to drastic effects on both pollinator and plant populations (Aizen & Feinsinger 1994; Franceschinelli *et al.* 2015). While

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analyzing edge effects on the pollination and reproduction of Meliaceae species in the Atlantic Forest of southeastern Brazil, Franceschinelli *et al.* (2015) observed that the numbers of pollinators of the arboreal species examined were greater in the forest interior than at the forest edge.

Another factor that can affect the reproductive phenology of plants is climate change, which can alter flowering seasons, with consequent effects on plant-pollinator interactions (Hughes 2000; Hegland *et al.* 2009; Scaven & Rafferty 2013). These effects on the phenological behaviors of plants and the possible loss of synchrony between mutualistic partners indicate the necessity of better understanding pollination mechanisms and how they are affected by the characteristics of plant and pollinator populations (Hegland *et al.* 2009). A large proportion of our knowledge about phenological responses to climatic alterations has come from studies undertaken in temperate regions in the northern hemisphere, where the effects of global warming have been demonstrated in numerous studies (IPCC 2007).

Studies associating climate changes with alterations of phenological patterns at low latitudes in the southern hemisphere are still rare (Chuine 2010). As temperature variations are generally smaller in tropical and sub-tropical areas, rainfall has been identified as the principal phenological driver, especially in seasonal environments (Chambers *et al.* 2013). *El Niño* is a major source of climatic variation in tropical South America, mainly affecting rainfall regimes, with potential effects on phenological rhythms (Malhi & Wright 2004; Wright & Calderon 2006). Multiple year studies of reproductive phenology can help identifying the effects of *El Niño* and their roles as phenological drivers (Wright & Calderon 2006; Chambers *et al.* 2013).

The reproductive phenology and pollination of plants in the Chapada Diamantina Mountains (the northern extension of the Espinhaço Range in central-eastern Brazil) have been the subject of several studies (Funch *et al.* 2002; Ramos *et al.* 2005; Souza *et al.* 2012; Souza & Funch 2016). The mountains at the eastern edge of the Chapada Diamantina are covered by seasonal submontane forests (Atlantic Forest *sensu lato*) growing on deep latosols. These forests have experienced profound physical impacts in the last 30 years (Oliveira-Filho & Fontes 2000; Funch *et al.* 2008; Couto *et al.* 2011; Couto-Santos *et al.* 2015), including the installation of electrical transmission lines. Clearing during these installations has created extensive linear edges and caused strong impacts on the local floristic composition and on the abundances of arboreal species, including *Eschweilera tetrapetala* (Lecythidaceae), which has been found to be more abundant in the forest interior than along artificial edges (Couto-Santos *et al.* 2015).

The overall distribution of *E. tetrapetala* is quite restricted, being endemic to the forests on the eastern slopes of the Chapada Diamantina mountain range (Funch *et al.* 2008; Couto *et al.* 2011). Its conservation status is vulnerable (IUCN 2014) and negatively impacted mainly by deforestation (CNCFLORA 2012). Menezes (2017) observed that variables related to rainfall are the predictors that most contribute to the construction of models regarding the potential distribution of *E. tetrapetala*, with projected reductions of 75 % of areas climatically adequate for its growth by 2100. This projected reduction will be caused by temperature increases and rainfall reductions in northeastern Brazil, with consequent retractions of forested areas, including Atlantic Forest remnants (Torres & Marengo 2012; Colombo & Joly 2010).

Numerous species of the Lecythidaceae occur in seasonal environments with well-defined dry and rainy seasons, with flowering occurring in the driest season and fruiting at the beginning of the period with the highest rainfall (Mori 1988). This phenological reproductive pattern has been observed in *E. ovata* (Krause 2008), but not in *Eschweilera tenuifolia* (Maia & Piedade 2000). The genus *Eschweilera* is considered hyperdominant and requires specific habitat characteristics (Steege *et al.* 2013). Its pollination is associated with large bees, following the general pattern of the family (Prance 1976; Potascheff *et al.* 2013).

In light of the restricted distribution of *E. tetrapetala* in seasonal submontane forests along the eastern edge of the Chapada Diamantina, where different population densities are known to occur along forest edges and in the forest interior (Couto-Santos *et al.* 2015), and where variables related to precipitation are the main predictors contributing to models of its potential distribution (Menezes 2017), we investigated the reproductive phenology *E. tetrapetala* and its floral visitors to address the following questions: i) Are the flowering and fruiting phenophases of *E. tetrapetala* associated with environmental factors? ii) Are there differences in the reproductive phenologies of individuals growing in the forest interior and along the forest edge? iii) If such differences exist, do they affect fruit set in interior and edge sites? iv) Are there variations in the species richness of floral visitors to *E. tetrapetala* plants between interior and edge environments? v) Are there reproductive phenological variations associated with *El Niño*, as rainfall variations associated with that phenomenon are known to have important roles in regulating phenological rhythms (Wright & Calderon 2006)? Our main hypothesis was that the reproductive phenology of *E. tetrapetala* would be affected by inter-annual variations in rainfall related to the *El Niño* phenomenon and by forest edge-interior environmental contexts. Additionally, we hypothesize that the edge context would negatively affect the richness of floral visitors of *E. tetrapetala*.

Materials and methods

Study area and the target species

The present study was undertaken in an area of seasonal submontane forest in the municipality of Lençóis

(12º28’31”S 41º23’14’’W), in the Chapada Diamantina National Park, Bahia State, Brazil. The region has a tropical climate (type Aw by the Köppen system), with a rainy season concentrated in the Austral summer (between December and April), and a dry winter season (between July and August). The mean monthly precipitation generally varies between 35 mm (July and August) and 184 mm (December), with the mean annual precipitation varying between 700 and 1300 mm. Mean monthly temperatures vary between 18 ºC (April to September) and 22 ºC (October to February) (Azevedo & Silva 2000; Alvares *et al.* 2014). Climatic data of total monthly precipitation, mean monthly temperatures, mean monthly relative humidity of the air, mean monthly solar radiation, and mean monthly photoperiod (Fig. 1A-D) were obtained from the INMET (2017) database of the Lençóis-BA weather station (12°27’36”S 41°22’48”W).

Northeastern Brazil experiences high inter-annual variations in total rainfall, partially due to the *El Niño* and *La Niña* meteorological phenomena. *El Niño* cycles alter the global climate, modifying the rainfall regimes in tropical and semitropical regions, with northeastern Brazil experiencing diminished cloud cover and reduced rainfall (Marengo *et al.* 2011). During the years 2015 and 2016, the region was affected by a strong *El Niño* event that initiated in May/2015 and reached its maximum between October/2015 and January/2016, producing scenarios of extreme drought throughout central Bahia State – which was only surpassed in intensity by the *El Niño* event of 1997/1998 (INMET 2017).

Eschweilera tetrapetala Mori is a tree 5 - 20 m tall, with glabrous leaves with entire to slightly serrate leaf margins. The flowers are white and yellow, large and perfumed. The fruits (pyxis type) have oily seeds (Fig. 2A-E). The species is known as “sapucaia” in the Chapada Diamantina; its fruits are used in traditional craft works, and its seeds can be consumed by humans (Mori 1995; Funch *et al.* 2004).

Phenology

Phenological observations were performed on a monthly basis during three periods: the first period extended from January/2011 to December/2011; the second from January/2012 to December/2012; and the third from October/2015 to September/2016 (including the *El Niño* event). Phenological observations were made within 30 permanent random plots (10 x 10 m; total 0.3 ha) established by Couto-Santos *et al.* (2015), with 15 plots along the forest edge (0–100 m from an electrical line corridor) and 15 plots in the forest interior (>150 m from the edge). Couto-Santos *et al.* (2015) inventoried 55 individuals of *E. tetrapetala* (DBH≥5.0 cm) in the area. The numbers of individuals observed in the forest interior (n=49) and along the forest edge (n=6) reflected

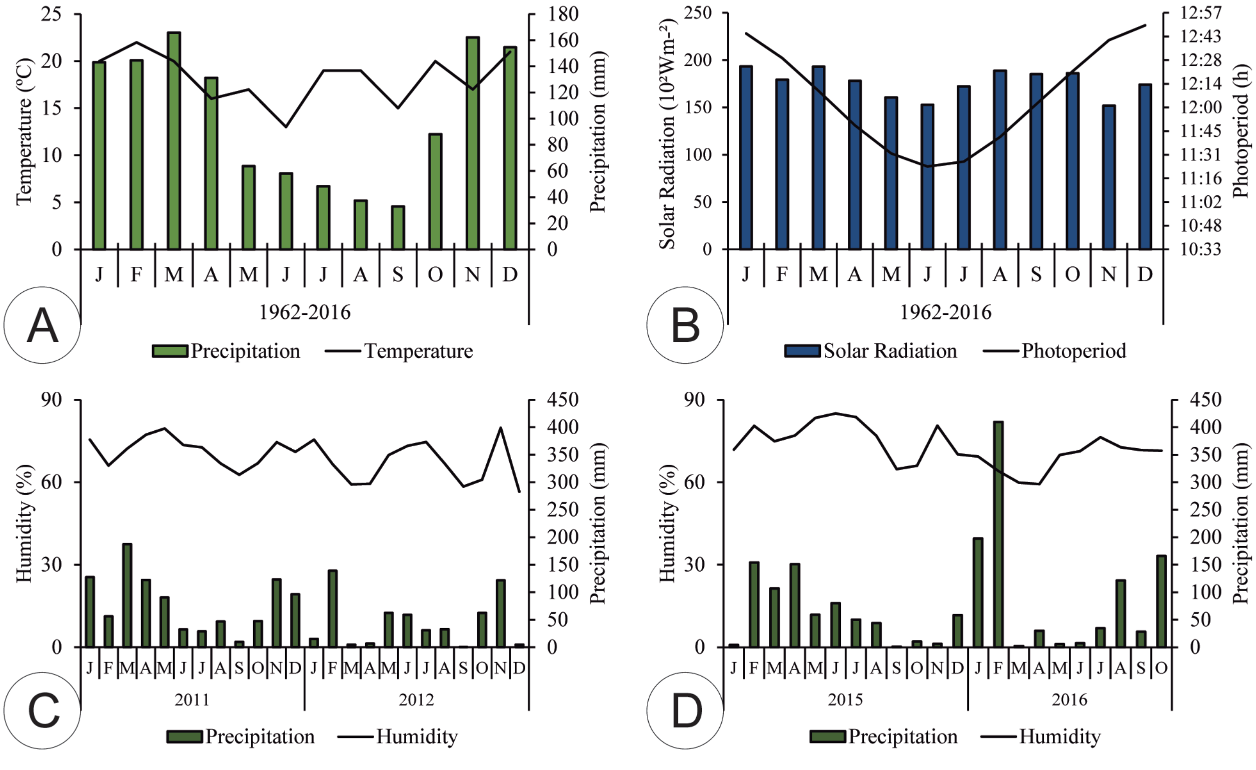

Figure 1. Environmental data from the region near Lençóis, Chapada Diamantina, Brazil. **A.** Precipitation and Temperature (1962-2016); **B.** Solar radiation and Photoperiod (1962-2016); **C.** Precipitation and Humidity (2011-2012); **D.** Precipitation and Humidity (2015-2016). Sources: Instituto Nacional de Meteorologia, and the Astronomical Applications Department of the U.S. Naval Observatory.

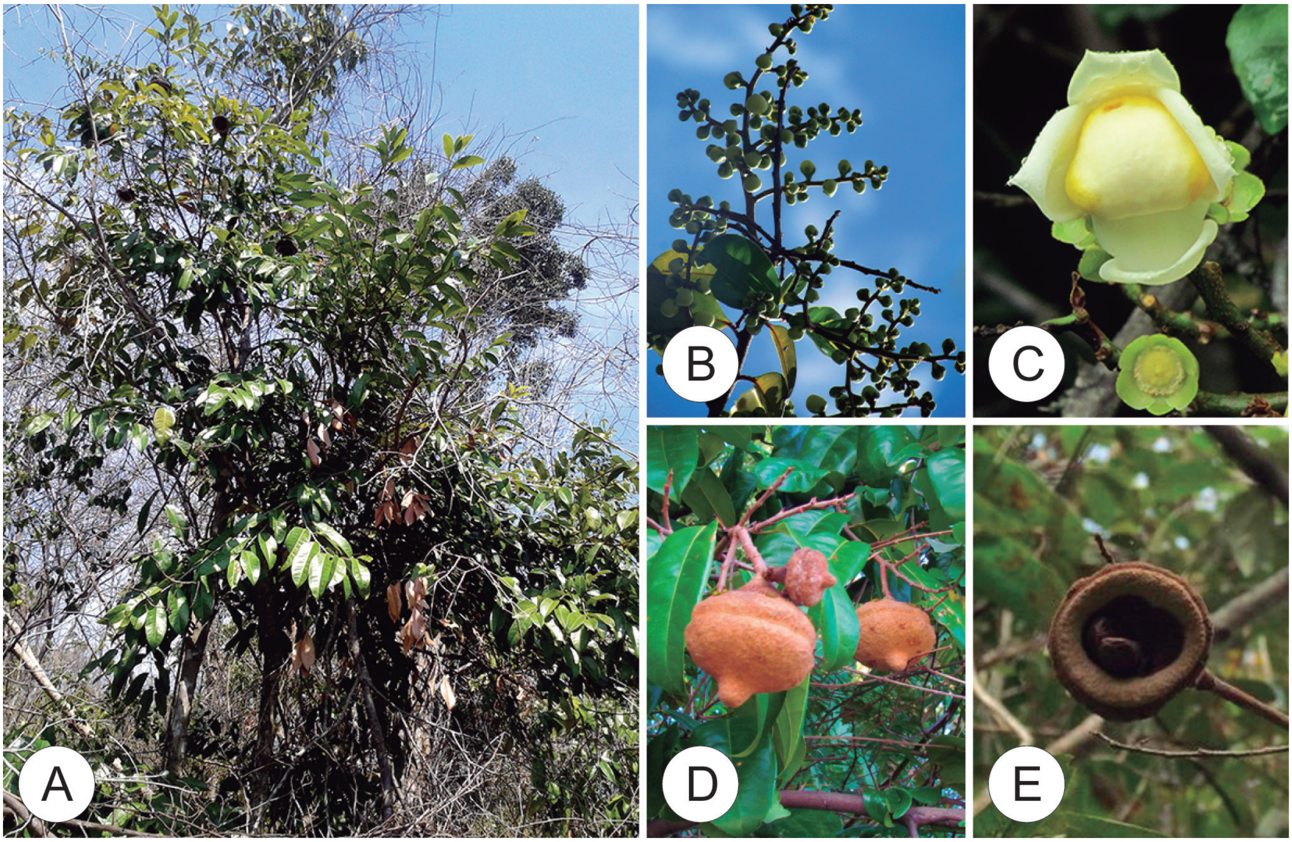

Figure 2. Habitat and observed phenophases of *Eschweilera tetrapetala* Mori: **A.** Habitat; **B.** Inflorescences; **C.** Flower; **D.** Immature fruits; **E.** Mature fruit, during dispersal.

their densities in our study area, with that species being significantly more abundant in the forest interior (Importance Value of 42.3 %; Relative Density 22.5 %) than along the forest edge (Importance Value 6.53 %; Relative Density 2.49 %) (Couto-Santos *et al.* 2015). We chose thirty individuals to follow their phenological events.

The phenophases monitored were: production of floral buds, opened flowers, and immature and mature fruits (Fig. 2B-E). The intensity of each phenophase was estimated by establishing classes from 0 to 4, with 25 % intervals between them, according to the semi-quantitative method of Founier (1974). The phenological patterns were described following Newstrom *et al.* (1994), based on the frequencies and durations of those episodes.

We also counted the total number of fruits produced by each individual of E. *tetrapetala* on a monthly basis to estimate fruit set.

Floral visitors and potential pollinators

We made focal observations of floral visitors on five individual trees (two along the forest edge and three in the forest interior). The low number of individuals monitored reflected their heights, the low intensity of floral production, and the low flowering synchrony of the population, with few individuals flowering at the same time. Daytime observations were made during 15 minutes per hour, totally 24 hours along the forest edge and 36 hours in the forest interior, in April/2016 and June/2017. We recorded floral visitor behaviors, their contact with reproductive structures, the floral resource consumed, the numbers of flowers visited by each animal, and the durations of the visits.

Any floral visitor landing on a flower was considered a visit. The insects were collected using an insect net and then sacrificed using ethyl acetate vapors. All floral visitors collected were sent to specialists for taxonomic identification, and subsequently mounted in the laboratory and deposited in the Johann Becker Entomology Collection at the Zoology Museum of the State University of Bahia at Feira Santana (MZUEFS). Floral visitors observed in the forest interior could not be collected due to the heights of the trees, but were photographed and/or filmed.

Floral visitors were classified based on the terminology proposed by Inouye (1980), following the identification of legitimate or illegitimate visits, as: i) pollinators (legitimate visitors), which demonstrated behavior conducive to effective pollination, including visits to the flowers during their period of pollen availability, and lifting the androecial hood that restricts access to the nectar so that the dorsal portion of the insect touches the stamen whorl and the stigma (Mori *et al.* 1978); ii) thieves (illegitimate visitors), visitors that collected floral resources, without damaging the flowers but without specific pollination behavior; iii) robbers (illegitimate visitors), visitors that damage floral tissues while collecting floral resources, thus reducing the attractiveness of those flowers.

Data analyses

Reproductive phenological intensity and its correlation with environmental variables

The intensity of the reproductive phenologies and their correlations with environmental variables were analyzed using Cross Correlation Analysis to evaluate the lag period between the phenophases studied and the environmental factors considered (photoperiod, temperature, relative humidity of the air, solar radiation, and precipitation). We considered in these analyses only significant results ($p<0.05$) and those with plausible biological effects. The cross correlation analyses were carried out using free access PAST version 2.17c software (Hammer *et al.* 2001). The Kruskal-Wallis and Wilcoxon signed-rank tests were used to evaluate if there were inter-annual variations in the intensities of the phenological events and if they were repeated in subsequent years (Zar 2010; Morellato *et al.* 2010). The Kruskal-Wallis tests were performed using BioEstat 5.3 software (Ayres *et al.* 2007). Spearman correlations (r_s) were performed using R software, version 3.2.3, (R Core Team 2014).

Seasonality

The seasonality of the phenological data (flowering and fruiting) was analyzed based on circular statistics, in which the months of the year were converted into 30° angle intervals (Morellato *et al.* 2010). For each phenophase, we calculated: (i) the mean angle, which represents the mean date of the phenological activity considered; (ii) the length of the *r vector*, which reflects aggregation of the dates (event synchrony) as well as the seasonality of the species studied (with high *r* values [> 0.5] indicating aggregation and therefore the seasonality of the phenological event under consideration); (iii) the Rayleigh test (z) to determine if the dates demonstrated uniform distributions throughout the year (Zar 2010). The Mardia-Watson-Wheeler (W) test was used to compare the mean dates of each phenophase during the study periods (Batschelet 1981). This latter test is nonparametric (and an alternative to the Watson-Williams (F) test, which is parametric) and compares how similar two or more distributions appear to be, with values of $p < 0.05$ rejecting the null hypothesis, under the assumption that the sets of dates demonstrate distinct distributions (Zar 2010). The circular statistical analyses and the Mardia-Watson-Wheeler tests were performed using R software, with the addition of the "circular" package version 3.2.3 (R Core Tean 2014).

Reproductive phenology and the production of fruits in the forest interior and edge

One-Way ANOVA tests were used to analyze the differences between the numbers of *E. tetrapetala* individuals that flowered and fructified in the forest edge and in the forest interior, as well as fruit set in both environments.

Floral visitors in the forest edge and interior

The Wilcoxon-Mann-Whitney test was used to analyze the differences in the species richness of floral visitors to *E. tetrapetala* between the forest edge and forest interior. The Wilcoxon-Mann-Whitney and ANOVA One-Way tests were performed using BioEstat 5.3 software (Ayres *et al.* 2007).

Results

Phenology

In general, the reproductive events of *E. tetrapetala* were seasonal, with low intensities during all of the observed phases (Fig. 3A-D, Tab. 1). The beginning of flowering changed during the observation period, occurring during the rainy season (between December and January) in the first and second years (2011-2013), and during the transition from the dry to rainy season (between April and July/2016) in the third year (2015-2016), during the occurrence of an *El Niño* event. This shift was marked by significant inter-annual variations of the mean dates of floral budding and immature and mature fruit stages (Tab. 1; Tab. 2). Significant differences were observed in mean mature fruit production among the different years ($W=7.78$, $p=0.02$), varying from August (in the first and second year) to November (in the third year, during the *El Niño* event) (Tab. 1; Tab. 2). Inter-annual variations were observed in floral budding and immature fruit intensity between the second (2012) and third years (2015-2016), while mature fruit production exhibited inter-annual variations between the first (2011) and third year (Tab. 2).

During the first and second years, *E. tetrapetala* fructified only in the forest interior (Fig. 3A). During the third year, within the *El Niño* event, buds, open flowers and immature fruit production were observed in the edge site, without significant differences between the edge and interior (Tab. 3). Significant differences were observed, however, for fruit set in the edge ($n=7$) and forest interior ($n=27$) during the third year ($F= 79.78$, $GL=1$, $p<0.05$).

The flowering and fruiting of *E. tetrapetala* appeared to be associated with all of the environmental factors

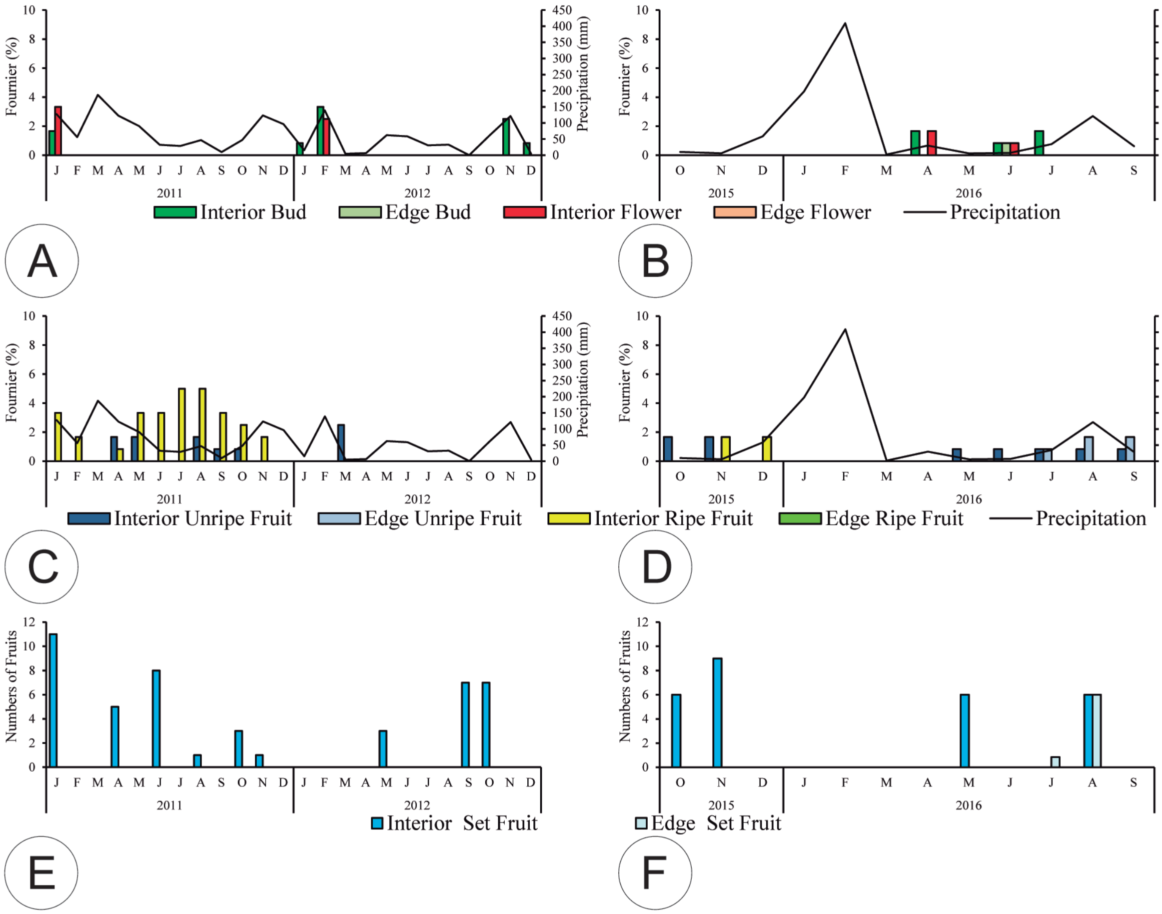

Figure 3. Reproductive phenology of *Eschweilera tetrapetala* Mori, in the interior and along the edge of a seasonal submontane forest, in the municipality of Lençóis, Chapada Diamantina, Bahia State, Brazil. **A.** Floral buds and open flowers (2011-2012); **B.** Floral buds and open flowers (2015-2016); **C.** Unripe and ripe fruits (2011-2012); **D.** Unripe and ripe fruits (2015-2016); **E.** Set fruit (2011-2012); **F.** Set fruit (2015-2016). Please see the PDF version for color reference.

Table 1. Results of circular statistical analyses for the occurrence of seasonal flowering and fruiting of *Eschweilera tetrapetala* Mori in a seasonal submontane forest, Lençóis, Chapada Diamantina, Bahia State, Brazil. Phenological event observations (N), during three years of observations.

Year	Statistical parameters	Buds	Flower	Immature fruit	Mature fruit
1st year (January to December/2011)	Observations (N)	2	2	18	5
	Mean vector (μ)	0°	0°	195°	230.10°
	Mean date	01/Jan.	01/Jan.	16/Jul.	21/Aug.
	Mean length of vector (r)	1	1	0.39	0.16
	Circular standard error	0°	0°	52.07°	72.08°
	Rayleigh Test (p)	0.13	0.13	0.49	0.63
2nd year (January to December/2012)	Observations (N)	4	1	1	0
	Mean vector (μ)	345°	30°	60°	
	Mean date	15/Dec.	30/Jan.	29/Feb.	
	Mean length of vector (r)	0.84	1	1	
	Circular standard error	22.56°	0°	0°	
	Rayleigh Test (p)	0.051	0.051	0.51	
3rd year (October/2015 to September/2016)	Observations (N)	6	3	14	4
	Mean vector (μ)	141.20°	109.11°	225°	315°
	Mean date	22/May	20/Apr.	15/Aug.	15/Nov.
	Mean length of vector (r)	0.79	0.88	0.65	0.96
	Circular standard error	25.36°	18.92°	34.84°	34.86°
	Rayleigh Test (p)	0.001	0.001	0.001	0.001

Tabela 2. Results of Kruskal-Wallis (H), Willcoxon (Z) tests for Fournier intensity and Watson-Weller(W) test for variation in the mean dates of *Eschweilera tetrapetala* Mori reproductive phenophases, in a seasonal submontane forest,Lençóis, Chapada Diamantina, Bahia State, Brazil, over three years of observations. The first year extended from January to December/2011; the second from January to December/2012; and the third from October/2015 to September/2016 (during the *El Niño* event).

Years	Statistical Tests	Budding	Flower	Unripe Fruit	Ripe Fruit
2011x2012	Watson-Weller	W=3.75	W=2	W=6.63	_
		p=0.15	p=0.36	p=0.04	_
	Willcoxon	Z= 1.19	Z=0.44	Z= 0.94	Z=2.71
		p=0.27	p=0.64	p=0.34	p=0.006
2011x2015-2016	Watson-Weller	W=3.98	W=3.98	W=1.08	W=7.78
		p=0.13	p=0.13	p=0.58	p=0.02
	Willcoxon	Z= 0.91	Z=0.26	Z=1.05	Z=2.14
		p=0.33	p=0.78	p=0.29	p=0.03
2012x2015-2016	Watson-Weller	W=7.10	W=2	W=7.78	_
		p=0.02	p=0.36	p=0.02	_
	Willcoxon	Z=0.73	Z= 0.80	Z=1.54	Z=0.76
		p=0.49	p=0.42	p=0.12	p=0.46
2011x2012x2015-2016	Watson-Weller	W=10.47	W=7.63	W=9.15	W=7.78
		p=0.03	p=0.10	p=0.05	p=0.02
	Kruskal-Wallis	H= 1.13	H=0.11	H=4.22	H= 9.80
		p=0.56	p=0.94	p=0.12	p=0.001

Table 3. Results of the circular statistical analyses for the occurrence of seasonal flowering and fruiting of *Eschweilera tetrapetala* Mori (October/2015 to September/2016) in the interior and edge contexts of a seasonal submontane forest, Lençóis, Chapada Diamantina, Bahia State, Brazil. Phenological event observation (N).

Environmental Contexts	Statistical parameters	Budding	Immature fruit
Edge	Observations (N)	1	5
	Mean vector (μ)	01/jun	07/ago
	Mean date	150°	216.20°
	Mean length of vector (r)	1	0.92
	Circular standard error	0°	14.90°
	Rayleigh Test (p)	0.51	0.005
Interior	Observations (N)	5	9
	Mean vector (μ)	19/mai	24/ago
	Mean date	138.90°	233.79°
	Mean length of vector (r)	0.76	0.51
	Circular standard error	27.93°	43.56°
	Rayleigh Test (p)	0.04	0.09
	Watson Weller	W=2.7745	W=2
		p= 0.24	p= 0.36
	One-way Anova	F=1.87	F=1.11
		p=0.18	p=0.30

analyzed. Flowering demonstrated positive correlations with precipitation, photoperiod, and solar radiation during the first and second years. During the *El Niño* event, flowering was positively correlated with precipitation and humidity, and negatively correlated with photoperiod and temperature. Fruiting was observed to be positively correlated with precipitation and negatively correlated with temperature, photoperiod, and solar radiation during the first and second years. During the *El Niño* event, fruiting was positively correlated with humidity and solar radiation, and negatively correlated with temperature and photoperiod (Tab. 4).

Floral visitors and pollinators

Bees and butterflies were observed visiting *E. tetrapetala* flowers. *Xylocopa* sp. was observed only in the forest interior, totaling 18 visits. This bee was the only floral visitor classified as a pollinator, as it lifted the androecial hood to collect nectar, and the dorsal portion of its body contacted the reproductive structures of the flower. *Xylocopa* sp. visits occurred between 07h00min and 11h00min, with durations of approximately 18 seconds each. Individuals of *Xylocopa* sp. were observed flying above the canopies of *E. tetrapetala*

Table 4. Results of the cross correlation analysis of the Fournier intensities of the reproductive phenophases of *Eschweilera tetrapetala* Mori as a function of total monthly rainfall, mean relative humidity of the air, photoperiod, solar radiation, and temperature for each year in a seasonal submontane forest, Lençóis, Chapada Diamantina, Bahia State, Brazil, over three years of observation, indicating the correlation coefficient (r) and the lag time (numbers of months) with which a given phenological variable follows a given meteorological variable. The Cross Correlation coefficients are significant ($p \leq 0.05$).

Year	Phenophase	Rainfall		Humidity		Photoperiod		Solar radiation		Temperature	
		r	Lag	r	Lag	r	Lag	r	Lag	r	Lag
Year 1 (January to December/2011)	Bud	-	-	-	-	-	-	0.66	3	-	-
	Flower	-	-	-	-	-	-	-	-	-	-
	Immature fruit	-	-	-	-	-	-	-0.7	3	-	-
	Mature fruit	0.71	0	-	-	-0.65	1	-	-	-0.78	-
Year 2 (January to December/2012)	Bud	0.77	0	-	-	0.59	1	-	-	-	-
	Flower	-	-	-	-	-	-	-	-	-	-
	Immature fruit	-	-	-	-	-	-	-	-	-	-
	Mature fruit	-	-	-	-	-	-	-	-	-	-
Year 3 (October/2015 to September/2016)	Bud	-	-	-		-0.67	0	-	-	-0.86	5
	Flower	0.78	2	0.85	5	-	-				
	Immature fruit	-	-	0.84	0	-0.74	1	-	-	-0.67	0
	Mature fruit	-	-	-	-	-	-	0.64	0	-	-

along the forest edge, but they were not observed visiting their flowers.

Trigona spinipes was observed in large numbers, primarily visiting the flowers of forest edge trees. These bees demonstrated behavior compatible with resource robbers, as they fed on the apical and lateral portions of the androecial hood, opening holes through which they could penetrate into the flowers and forage in their interiors. Visits by *Trigona spinipes* occurred between 05h00min and 16h00min, and lasted approximately 15 minutes each. Up to six bees were observed visiting a single flower at the same time, showing territorial and antagonistic behaviors in relation to other visitors. The frequencies of floral visits by *T. spinipes* in the forest interior were lower than along the forest edge, with only a single visit per flower, totaling 16 visits in the interior site and 220 visits along the forest edge.

We observed five species of Lepidoptera visiting the flowers of *E. tetrapetala*, but only in the forest interior. Those visitors showed thieving behavior, as they landed on the androecial hood, inserted their proboscis into the lateral sides of the androecial hood, and consumed nectar from flowers without contact with the reproductive structures.

The species richness in both environmental contexts were significantly distinct (U= 7, p=0.02), with seven species of floral visitors in the interior but only one along the forest edge.

Discussion

We investigated whether there were shifts in the reproductive phenology of *E. tetrapetala* associated with seasonality and the edge-interior contexts in a seasonal submontane forest in the Chapada Diamantina Mountains in northeastern Brazil. Additionally, we sought to verify if there were variations in the species richness of floral visitors to *E. tetrapetala* between the two environmental contexts. In agreement with our hypothesis, we found that the intensities of the reproductive events of *E. tetrapetala* were affected principally by inter-annual variations in rainfall related to the *El Niño* phenomenon. We also observed that the edge context affected flowering and fruiting intensity, fruit production, and the richness of floral visitors to *E. tetrapetala*. Our results highlight the relevance of rainfall seasonality in controlling phenological changes in *E. tetrapetala*. We also noted that differences in local conditions (forest edge and interior) can be important in determining the temporal patterns of *E. tetrapetala* and floral visits.

The phenological seasonality observed in *E. tetrapetala* was similar to that of other Lecythidaceae species such as *Eschweilera tenuifolia* (Maia & Piedade 2000), *Bertholletia excelsa* (Tonini 2011), and *Lecythis poiteaui* (Freitas *et al.* 2015). The pattern described by Mori (1988) for the Lecythidaceae, with flowering occurring during the dry season and fruiting at the beginning of the rainy season, was not observed in *E. tetrapetala*.

The inter-annual variations in the mean dates of flowering initiation and fruit maturation observed in *E. tetrapetala* were demonstrated by the Mardia-Watson-Wheeler test (W), possibly associated with climatic oscillations resulting from *El Niño* events during the third study period. Events associated with the *El Niño* phenomenon are a major source of climatic variation in the tropics, provoking long droughts, decreased cloud cover, as well as increases in solar radiation and environmental temperatures (Malhi & Wright 2004). Monitoring flower and seed production during annual cycles could help us to better understand the effects of climatic variations on plant reproduction, as the reproduction rates of many species accompany those inter-annual climatic variations and respond to *El Niño/La*

Niña oscillations (Wright & Calderon 2006). In the first and second years of the study, the flowering of *E. tetrapetala* occurred during the rainy season. In the third year, however, the *El Niño* phenomenon resulted in a long drought that extended from the beginning of 2015 until the beginning of 2016 (INMET 2017), apparently delaying flowering in *E. tetrapetala*, which occurred then during the transition from the rainy to the dry season.

The inter-annual variations in flowering and fruiting in *E. tetrapetala* were correlated with most of the environmental predictors analyzed, especially precipitation. As in many tropical species that produce flowers coinciding with increases in solar radiation, temperature, and photoperiod (Bhat 1992; Wright & Schaik 1994; Talora & Morellato 2000; Marchioretto *et al.* 2007), *E. tetrapetala* flowering showed correlations with solar radiation and photoperiod in some study years, but not with temperature. *E. tetrapetala* altered its flowering period to accompany rainfall oscillations provoked by the *El Niño* phenomenon.

Tropical species can maintain their floral buds in a quiescent state during periods of water stress but, after rehydration at the start of the rainy season, those buds expand and enter into anthesis (Borchert *et al.* 2004). As such, the availability of water resources appears to be a preponderant factor for determining the reproductive phenology of *E. tetrapetala,* as flowering was consistently found to occur after high rainfall in the study area. This observation was supported by cross correlation analyses, which demonstrated that flowering was associated with increases in precipitation and/or humidity.

Changes in the reproductive phenologies of plants can result in the temporal asynchrony of plant-pollinator interactions, with plant species flowering when pollinator activities have already concluded, or not yet initiated (Bartomeus *et al.* 2011; Forrest 2015). Such asynchrony can negatively affect plant and/or animal populations, reducing resource availability for animals and/or reducing the reproductive potentials of plants (Rusterholz & Erhardt 1998; Kudo *et al.* 2004; Thomsom 2010). Longer observation periods will be required to better define the interactions between abiotic and biotic factors, although *Wright* & Calderon (2006) noted that any reported relationships between *El Niño*/*La Niña* oscillations and living organisms will contribute to our understanding of directional changes in the dynamics of tropical forest species and their responses to climatic and anthropogenic alterations.

The linear edge negatively affected the population density of E. *tetrapetala* and its reproductive events, as the individuals in that context were not observed flowering during the first two study years, and produced reduced numbers of fruits in the third study period in relation to the forest interior. Numerous studies have demonstrated that edge effects reduce the availability of abiotic resources such as water and soil nutrients (Dunley *et al.* 2009; Athayde & Morellato 2014; Aizen & Feinsinger 1994; Franceschinelli *et al.* 2015), and diminish fruit set as compared to that seen in the forest interior (Dunley *et al.* 2009; Athayde & Morellato 2014).

Edge effects were also noticeable in terms of the richness of floral visitors to *E. tetrapetala*. Among the floral visitors of *E. tetrapetala, Xylocopa* sp. was the only insect classified as an effective pollinator, even though it showed a low visitation frequency and was not observed visiting individuals near the forest edge. *Xylocopa* sp. has been identified as a potential pollinator of other species of *Eschweilera* (Krause 2008; Potascheff *et al.* 2013) and of other genera of Lecythidaceae (e.g., *Couropita guianensis* and *Lecythis lurida* (Mori *et al.* 1978; Ormond *et al.* 1981)). Pollination by bees is widely observed in Lecythidaceae (Knudsen & Mori 1996), and most studies of the genus *Eschweilera* have reported pollination by Hymenoptera (Prance 1976; Mori *et al.* 1978; Gamboa-Gaitán 1997; Krause 2008; Potascheff *et al.* 2013). According to Mori & Prance (1981), bees of the Euglossinae group that have long glossa and are able to reach the nectar in the coiled hood (e.g., *E. grandiflora* and *E. decolorans*), but they were not observed visiting *Eschweilera tetrapetala*.

The territorial behavior of *Trigona* species represents a very common defense strategy among social insects (Nieh *et al.* 2005) and has been reported in other studies involving species of Lecythidaceae (Santos & Absy 2010; Potascheff *et al.* 2013) as well as other tropical families (in which those bees were classified as robbers) (Roubik 1982). Interestingly, resource pillaging by melipona bees, as well as their aggressive behavior, have both been evaluated as positive factors in some studies. Decreasing resources offered to pollinators force them to visit more flowers to obtain their required energetic resources, enhancing the chances of cross pollination (e.g., Malloof & Inouye 2000; Silva *et al.* 2014). We observed aggressive behavior by *T. spinipes* bees only at the forest edge, which may explain why *Xylocopa* sp. was not observed visiting flowers in that environment context. The frequency of *T. spinipes* diminished significantly in the forest interior, favoring the presence of the effective pollinator *Xylocopa sp.*

During the third study period, when *E. tetrapetala* flowered and fructified both at the forest edge and in its interior, there were significant differences in fruit production between those two contexts. The reduced fruit production observed at the forest edge may be associated with the absence of effective pollinators in that context. The observed differences in floral visitor frequencies and behaviors may alter the quality and quantities of pollen grains deposited on the stigmas and, consequently, fruit and seed production (Rathcke & Jules 1993). Additionally, most studies of the reproductive systems of Lecythidaceae have reported self-incompatible species, and without the presence of pollinators there would be no cross pollination and consequently little or no fruit formation (Moritz 1984; Lepsch-Cunha & Mori 1999; Gusson *et al.* 2006; Mori & Kallunki 1976; Potascheff *et al.* 2013). Although low fruit set has previously been noted in the Lecythidaceae family

(Potascheff *et al.* 2013), fruit set by *E. tetrapetala* was even lower at the edge than in the interior.

Eschweilera tetrapetala is more abundant in the submontane forest interior (Couto-Santos *et al.* 2015), providing evidence that it is quite sensitive to niche alterations. It is important to note that, like most of the taxa of Lecythidaceae, *E. tetrapetala* requires insect pollinators for cross pollination and fruit set (Moritz 1984; Lepsch-Cunha & Mori 1999; Gusson *et al.* 2006; Mori & Kallunki 1976; Potascheff *et al.* 2013). Decreases in successful reproduction in fragmented forest environments have been associated with decreases in the qualities and quantities of pollinators found there (Aguillar & Galleto 2004). Similar results were observed with *Cabralea canjerana* (Meliaceae), which was visited by fewer pollinators, and demonstrated limited reproductive success in forest fragments when compared to continuous areas of Atlantic Forest (Franceschinelli *et al.* 2015).

In conclusion, we confirmed our general hypotheses that *E. tetrapetala* demonstrated inter-annual variations in the intensity and seasonality of flowering and fruit production, possibly linked to climatic alterations due to *El Niño*-provoked rainfall variations during the study period. We also observed that flowering and fruiting were more intense in the forest interior. Additionally, our study demonstrated how climatic changes (due to *El Niño*) and anthropogenic alterations (in this case related to edge creation) can influence both resource robbers and pollinators. Our study complemented existing knowledge of the reproductive phenology of Lecythidaceae and its floral visitors, and contributed to our understanding of the relative importance of two sources of variability (*El Niño* and edge effects) to the reproductive phenology of tropical plants.

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