Research Article

Edge effects on the phenology of the guamirim, *Myrcia guianensis* (Myrtaceae), a cerrado tree, Brazil

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Abstract

The Brazilian cerrado, a hotspot of biodiversity, has suffered intense fragmentation in the last decades with an associated increase in areas subjected to edge effects. Plant phenology may be influenced by abiotic changes induced by edge effects, such as increases in temperature and light. We studied the phenology of the guamirim (*Myrcia guianensis*, *Myrtaceae*) and its relation to local abiotic factors in a Brazilian cerrado area between 2005 and 2011, aiming to answer: (i) whether *M. guianensis* phenology differs between the edge and the interior and/or between cardinal orientations at the study site, given that environments facing east are lighter and warmer than environments facing south; and (ii) how microenvironmental factors influence the observed phenological patterns. We sampled 92 individuals in 36 transects (25m x 2m), distributed along the edge and in the interior (100m from the edge) of the east and south faces. *Myrcia guianensis* presented seasonal patterns of leafing and reproduction, but only reproduction was influenced by microenvironmental conditions. Individuals on the east edge — the warmest and driest environment with the most light — presented with the highest synchrony and intensity of reproductive phenophases, followed by the east interior, south interior and south edge. Flowering and fruiting onset and peak dates occurred around 20 days earlier on the east edge than the south face. Edge conditions, primarily cardinal orientation, and associated higher temperatures and light incidence influenced the reproductive phenology of *M. guianensis* and the onset of flowering and fruiting. We suggest that edges could be used to evaluate plant responses to the temperature increases predicted for future climate change scenarios.

Key-words: fragmentation; cerrado; microenvironmental factors; climate change; population phenology

Resumo

O cerrado brasileiro, um *hotspot* de biodiversidade, vem sofrendo intensa fragmentação nas últimas décadas, aumentando as áreas sujeitas ao efeito de borda. A fenologia das plantas é influenciada por mudanças nas condições abióticas causadas por esses efeitos, como o aumento da luminosidade e temperatura. Em uma área de cerrado estudamos a fenologia do guamirim (*Myrcia guianensis,* Myrtaceae), de 2005 a 2011, e sua relação com fatores abióticos locais, verificando: (i) se a fenologia de *M. guianensis* difere entre borda e interior e/ou entre ambientes com diferentes orientações cardeais (ambientes voltados para Leste são mais iluminados e quentes em relação aos voltados para Sul da área de estudo); e (ii) qual é a influência dos fatores microambientais nos padrões fenológicos. Amostramos 92 indivíduos em 36 transectos (25x2m), distribuídos ao longo da borda e interior (100m da borda) dos lados leste e sul da área de estudo. *M. guianensis* apresentou padrões sazonais para as fenofases vegetativas e reprodutivas, mas somente as reprodutivas foram influenciadas pelo microclima. Indivíduos da borda leste, ambiente mais quente, seco e iluminado, apresentaram maior sincronia e intensidade das fenofases reprodutivas, seguido do interior Leste, interior Sul e borda Sul. Datas de início e pico de floração e frutificação ocorreram 20 dias antes na borda Leste em relação à borda e interior Sul. Condições ambientais da borda e a orientação cardeal, associados a maiores temperaturas e luminosidade, influenciaram a fenologia reprodutiva de *M. guianensis* e anteciparam o início da floração e frutificação. Sugerimos que as bordas podem ser utilizadas para avaliarmos repostas das plantas ao aumento de temperatura decorrente das mudanças climáticas globais.

Palavras-chave: fragmentação; cerrado; fatores microambientais; mudanças climáticas; fenologia de população

Introduction

The Brazilian Cerrado covers an area of more than 2 million km² and is the richest and most threatened savanna in the world [1]. Since the 1950s, it has suffered intense fragmentation due to the advancement of the agricultural frontier [2]. This process has transformed the cerrado landscape into a series of isolated patches [3], and is one of the main threats to biodiversity in tropical woodlands [4, 5]. The reduction of natural areas covered by native vegetation results in a mosaic where natural vegetation is surrounded by a contrasting matrix [3, 6]. This process increases the quantity of edges, exposing organisms to what are known as edge effects [5, 7].

Edge effects can be classified into abiotic, direct and indirect biological processes [4]. The first process involves changes in environmental conditions such as temperature and humidity as a response to conditions near the contrasting matrix. The second is related to changes in species abundance and distribution as a result of the combination of changes in physical conditions and the physiological limits of each species. The last process involves changes in species interactions such as predation, competition and herbivory [4]. The assumption is that variations in abiotic and biotic factors drive changes in a plant community from the edge towards the interior [6-9], probably affecting the reproductive cycles of plants [10-12]. The influence of edges could also be related to the cardinal orientation, which determines the amount of exposure to solar radiation [4, 12, 13] and, therefore, influences the strength of the edge effects on microenvironmental conditions [14]. For instance, Ries *et al.* [14] stressed that abiotic responses to cardinal orientation are stronger than plant structure and diversity responses. However, few studies have addressed cardinal orientation and edge effects.

Many studies have reported on edge effects in tropical forests, including their influence on plants' phenological patterns, reproductive success and plant-animal interactions [11, 14-16], but the extension and consequences of edge effects have been poorly investigated in savannas [13-14,17], with most studies focusing on invasion by exotic species [e.g. 18-20]. Although one study indicated that the invasion of African grasses at the edges of savanna fragments was a more evident effect than changes in microclimate [20], Dodonov *et al.* [17] found edge influences on microclimate in woody savannas physiognomies, mainly related to an increase of temperature towards the edges.

Temperature increases on cerrado edges, registered by Athayde *et al.* [21], influenced flowering patterns and reduced the fruit set of angico-do-cerrado (*Anadenanthera peregrina*) [21]. Differences in light incidence also affected the reproductive pattern of individuals of the pimenta-de-macaco (*Xylopia aromatica)*, a cerrado tree, with more activity and synchrony noted in environments where there was more light [13].

The study of edge effects on plant phenology is relevant because of their influence on biological processes, but it can also bring new insights into plant responses to climate change [11] as temperature increase is one of the expected changes induced by edge effects [22]. Future climate change scenarios for the tropics uniformly predict increasing temperatures [23]. Thus, we could consider plant phenological shifts in response to edge conditions as representative of plant responses to future global climate changes.

In this study, we investigated how vegetative and reproductive phenology differs in relation to edge effects in cerrado vegetation, focussing on *Myrcia guianensis* (Aubl.) DC. (Myrtaceae), also known as guamirim*,* a widely distributed and representative species in the Brazilian cerrado [24]. We analyzed the phenology of *M. guianensis* in order to address the following questions: (i) Does the phenology of *M. guianensis* differ from the edge to the interior and, if so, does the cardinal orientation of the east-facing edge (which are warmer and have more light) and the south-facing one (which are cooler with less light) affect the differences? (ii) Do microenvironmental variables influence the patterns and the intensity of phenophases along the edge and in the interior as well as on the east and south faces?

Methods

Study area

This research took place in a cerrado remnant of 260 ha, located at Fazenda São José da Conquista in the municipality of Itirapina, São Paulo State, southeastern Brazil (22º 10' 31.41''S; 47° 52' 26.1 3''W; 610 m a.s.l.) (Fig. 1). The climate is seasonal, with a warm and wet season from October to March and a dry, cold season from April to September. During the study period, from January 2005 to December 2011, the climate was similar each year, consistent with the seasonal pattern described for the region (Fig 2, [13]). Meteorological data were provided by the climatic station at Centro de Recursos Hídricos e Ecologia Aplicada (CHREA), University of São Paulo (USP), 4 km from the study area. The vegetation in the study area is a cerrado *sensu stricto* [25], which is a savanna vegetation characterized by the presence of a continuous herbaceous layer and small, leaning, twisted trees with irregular and twisted ramifications reaching 6 to 7 meters in height. The vegetation may become denser in some parts, with a reduced herbaceous layer and some taller trees reaching up to 12 meters in height [13, 24].

The area is a rectangular cerrado remnant with sides facing the four cardinal directions. The four edges were established approximately 30 years ago. The study was conducted at the edges and in the interiors of the east and south faces of the study site. We named the four environments as follows: east edge (EE), east interior (EI), south edge (SE) and south interior (SI) (Appendix 1). Historically, the south edge faced a pasture matrix. Since 2008, however, it has been facing a sugarcane plantation. The east edge is separated from its adjacent matrix by a path 5 to 8 meters wide. The matrix is composed of another cerrado patch and pasture.

According to a previous study, east-facing environments have higher temperatures, more open vegetation, higher photosynthetic active radiation (PAR) incidence and lower relative humidity than south-facing environments [24]. These conditions are probably associated with cardinal orientation, which may increase the influence of the edge effects on the east face due to high daytime light incidence throughout the year [24]. The soil in the east facing site is significantly sandier and less acidic, and has a lower percentage of organic matter and cation-exchange capacity than the south facing site [24].
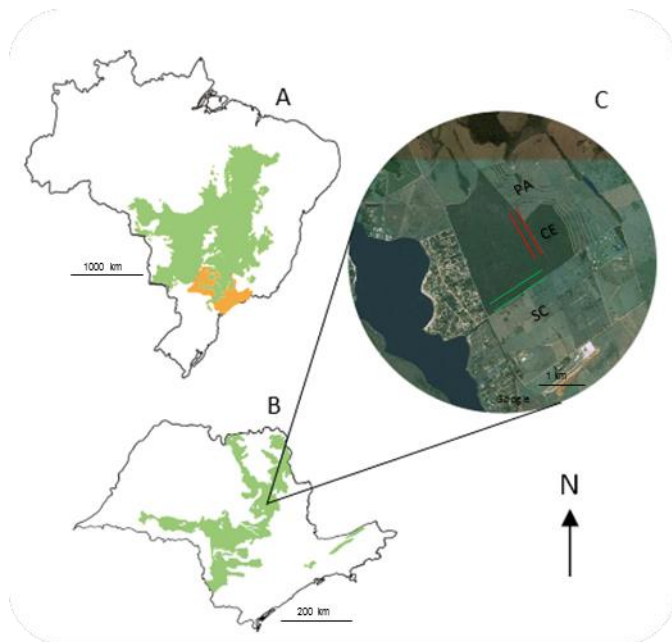
Fig. 1. Distribution of the Cerrado in Brazil, with São Paulo state colored in orange (A); distribution of the cerrado in São Paulo state and the position of the study site (B); and a detail of the study site located at Fazenda São José da Conquista in the municipality of Itirapina (260 ha) (C), red lines indicated east transects on edge and interior and green lines, south transects on edge and interior. SC - sugarcane matrix, CE - cerrado vegetation matrix, PA - pasture matrix. The arrow indicates North position. Cerrado distribution was based on the Brazilian Biome Map elaborated by the Brazilian Institute of Geography and Statistics (IBGE, 2004).

Fig. 2. Average rainfall and maximum (Tmax), mean (Tmean) and minimum (Tmin) temperatures for the period from January 2005 to December 2011 in the cerrado study site, southeastern Brazil.

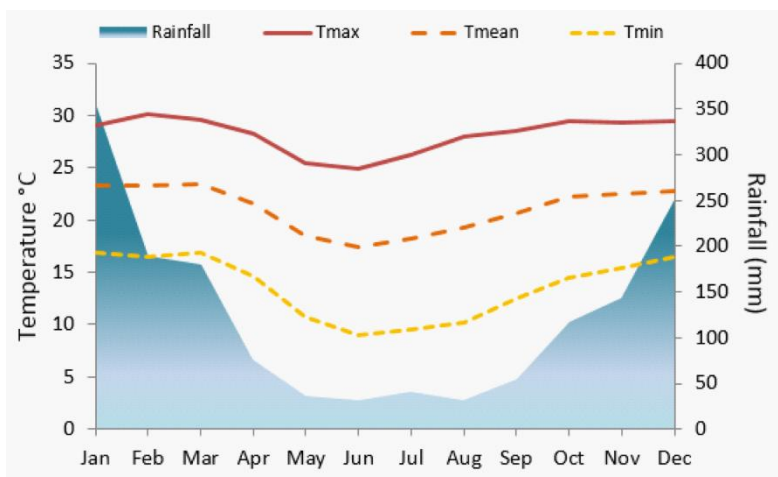*Study species*

Myrcia guianensis (Aubl.) Kuntze (Myrtaceae), commonly known as guamirim (as are most species of the *Myrcia* genus), was chosen due to its wide distribution and abundance at the study area and in the Cerrado in general [24]. The fruit is fleshy and is eaten by several bird species (Andre Guaraldo pers. comm.), and the flowers are visited by diverse species of insects [26, 27] and are mostly pollinated by bees. The fruit is mainly dispersed by birds and monkeys [26, 27]. The trees have rough, peeling, reddish bark. The leaves are simple, opposite and coriaceous. The flowers are white in terminal or axillary panicles, while the fruit consists of globular berries, red to dark purple, and about 3mm in diameter (Appendix 2). Myrtaceae is one of the richest families of species found in the Neotropics, comprising about 10-15% of the total tree species appearing in wet forests and in the eastern cerrado [28]. Despite the dominance of Myrtaceae in many Neotropical communities, few studies to date have addressed its phenology [26, 29-31].

Sampling and phenological observations

We recorded the phenological observations of individuals sampled in 36 transects of 25m x 2m, with a minimum distance of 50m between the transects. The transects were distributed within the interior (n=8) and along the edges (n=10) of the east and south faces of the study site. The transects on the edge were directly adjacent to the matrix, and the transects in the interior were located 100m from the edge. We considered only the individuals of *M. guianensis* with a circumference at the stem base equal to or larger than 3cm. In total, we sampled 92 individuals (32 on the east edge, 27 in the east interior, 13 on the south edge and 20 in the south interior).

Between January 2005 and December 2011 we conducted monthly phenological observations of flower buds and flowers (flowering), unripe fruit and ripe fruit (fruiting), leaf flush and leaf fall [32]. For each individual, we observed and estimated the intensity of each phenophase using a semi-quantitative index with 3 classes: 0 (absence), 1 (intermediate intensity) and 2 (peak of intensity) [33, 34].

Microenvironmental data

To understand how edges and cardinal orientation affect the intensity of the phenological phases of *M. guianensis* in each environment, we used the mean microenvironmental data previously collected by Reys *et al*. [24] from three points in each transect (every 8m). The variables included temperature, relative air humidity, incident photosynthetic active radiation (PAR), canopy openness and soil data (pH, organic matter, K, Ca, Mg, H+Al, Al, SB, CTC, V, S, B, Cu, Fe, Mn, Zn, proportions of clay, silt and coarse, medium and fine sand). All microenvironmental data were collected once in the dry season, in August 2006, and once in the wet season, in February 2007. For more details about the microenvironmental data collection, see Reys *et al*. [24].

Data analyses

To calculate the monthly intensity of each phenophase we adapted the Fournier Equation to consider two classes of intensity instead of four [35]. We calculated the sum of monthly intensity values for each individual divided by the total number of individuals multiplied by two. In order to describe the *M. guianensis* phenological pattern and check for possible differences between seasonal patterns among the four environments, we used the monthly mean percentage of intensity of the vegetative and reproductive phenophases, and summarized the seven years of observations (2005 to 2011) into a mean pattern over one year.

We determined the onset and peak dates of flowering and fruiting for all individuals of *M. guianensis* in each environment. We used circular statistics to test if the seasonality and synchrony of individuals differed among the environments [34, 36]. We calculated the mean angle (or mean date) of the frequency of individuals at the onset or peak of each phenophase in each environment, and tested the significance of the mean angle by applying the Rayleigh Z test, which indicates the occurrence of seasonality [34, 36]. The vector r length (indicating the concentration around the mean angle) for the onset and peak dates of each phenophase was used as an index of phenological synchrony among individuals in each environment [34, 36]. The vector r length has no units and varies from zero to one, with values closer to one indicating maximum synchrony among individuals. To test possible differences in the onset and peak dates among the environments, we applied the Watson-Williams F test for the most significant mean dates [36]. We performed all circular statistical analyses using ORIANA 4.0 (Kovach Computing Services).

In order to characterize the four environments according to their microenvironmental conditions, we used only microenvironmental data [24] from the transects which contained at least two individuals of *M. guianensis*. We first calculated the mean of the data for both dry and wet seasons to remove possible seasonal influences on the variables. We then used a Principal Component Analysis (PCA) to group the transects according to their microenvironmental conditions and to reduce the number of microclimatic variables, given that most of these microenvironmental features are correlated at different levels (collinearity) [4, 13]. Finally, we took the first and the second resultant principal components and performed linear regressions to understand how the microenvironmental differences of the transects influence the average intensity of each phenophase. We performed PCA and linear regressions in R (R Development Core Team 2011) using the "vegan" package [37].

Results

Phenology and climatic constraints

Overall, *M. guianensis* presented seasonal patterns for reproductive and vegetative phenophases (Fig. 3). In general, the patterns observed in different years were similar, with some variation in the intensity of phenophases (Appendix 3). Flowering occurred during the transition between dry and wet seasons, with flower buds from July to November and flowers from September to November, both peaking in September (Fig. 3A and 3B). Fruiting was observed mainly during the wet season. We found unripe fruit between September and January and ripe fruit between October and January, peaking in November (Fig. 3C and 3D).

Leaf flushing and leaf fall were observed throughout the year. However, leaf flushing was found mainly in the transition between dry and wet seasons, peaking in September, while leaf fall was found mainly in the dry season, peaking in June (Fig. 3E and 3F).

Phenology and the environments

The phenological patterns of each environment were similar, but with differences in the flowering and fruiting intensity. We observed the highest intensities of reproductive phenophases on the east face, and they were higher on the east edge than in the east interior (Fig. 3A to 3D). The intensity was also higher in the south interior than on the south edge (Fig. 3A to 3D). Although similar, vegetative phenophases presented a greater intensity of leaf flush on the east face and of leaf fall on the south face. Both of these phenophases were more intense in the interiors than at

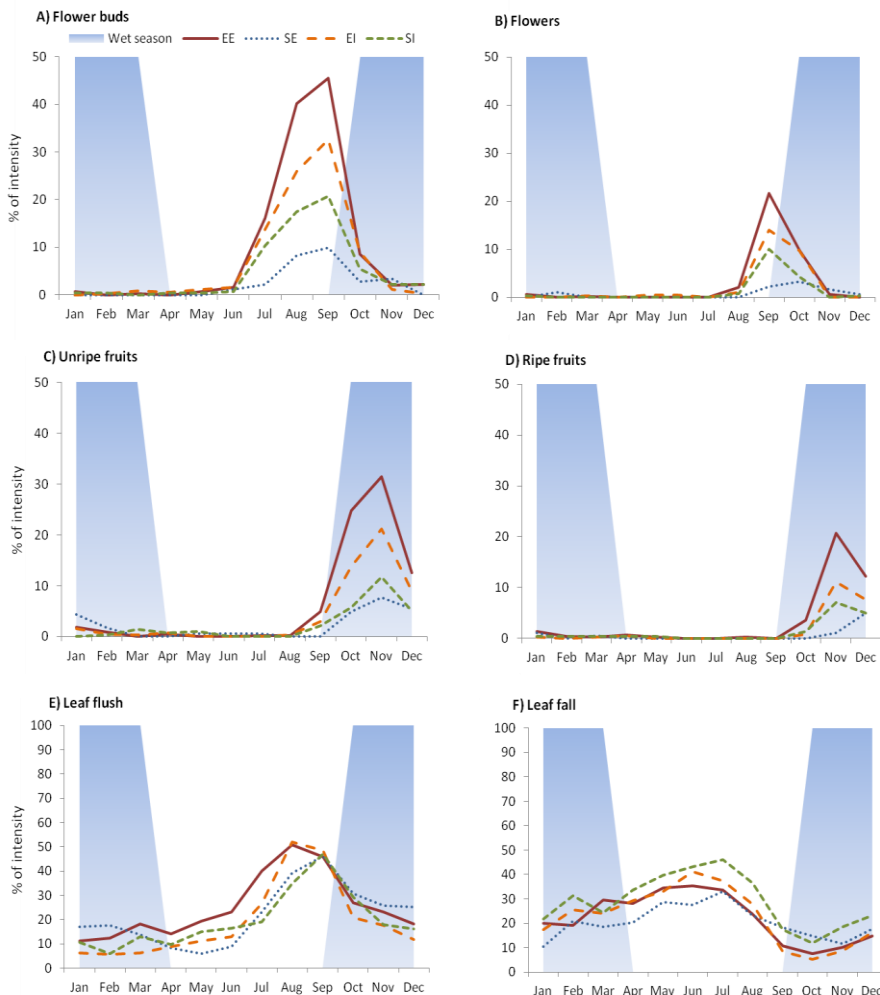the edges on both faces of the remnant (Fig. 3E and 3F).

Fig. 3. Average monthly intensity of flower buds, flowers, unripe fruits, ripe fruits, leaf flush and leaf fall from January 2005 to December 2011 in the individuals of *Myrcia guianensis* sampled in the east edge (EE), south edge (SE), east interior (EI) and south interior (SI) of the cerrado study site, southeastern Brazil. The blue area indicates the wet season.

M. guianensis showed significant seasonality in all environments for the onset and peak dates of reproductive phenophases (Rayleigh test, $p < 0.01$; Appendix 4). The synchrony of reproductive phenophases was higher in the east environments than the south ones (Fig 4, Table 1, Appendix 5). In general, the synchrony of the onset of reproductive phenophases was higher on the edge than in the interior, while the synchrony of the peak was similar on the edge and in the interior on the east face and higher in the interior than on the edge on the south face (Appendix 4).

The onset dates of reproductive phenophases were about 13 days earlier on the east face than the south (Fig. 4, Appendix 4). The mean onset of flowers, unripe and ripe fruit occurred 20 days earlier on the east edge than on the south face, with significant differences in the mean dates (Appendix 6). While the mean onset of flowers occurred on August 24 on the east edge, it was observed in September on the south face, first in the south interior (September 10th) and then on the south edge (September 16th) (Appendix 4). The mean onset dates of unripe fruit occurred on September 18th on the east edge and on September 22nd in the east interior, and 19 days later in the south interior (Appendix 4). The mean onset date of ripe fruit on the east edge was 11 days earlier than in the east interior and 25 days earlier than on the south edge (Appendix 4).
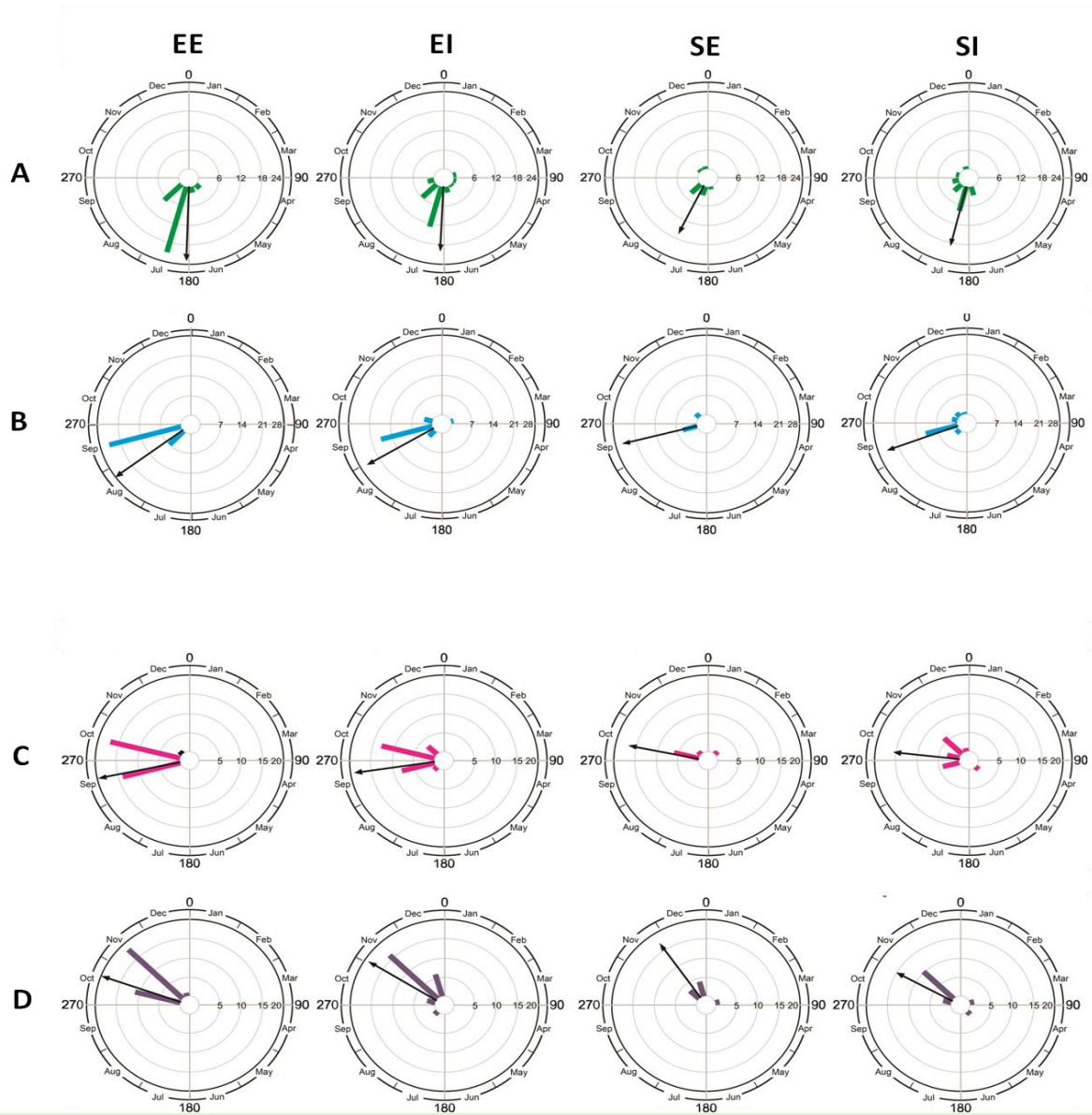
Fig. 4. Circular distribution of onset dates for flower buds (A), flower (B), unripe fruits (C) and ripe fruits (D), based on the mean pattern from January 2005 to December 2011 for *Myrcia guianensis* individuals sampled in the east edge (EE), east interior (EI), south edge (ES) and south interior (SI) of the cerrado study site. All mean angles are significant (Rayleigh test, p<0.001) and are represented by the arrows, while vector r (0 to 1) indicates the concentration around the mean angle.

The mean peak date of flowering and ripe fruit occurred around 10 days earlier in the east interior than in the south interior (Appendix 3, Table 1). The mean peak dates of flowers and unripe fruit occurred 25 days earlier on the east edge than on the south face, and the differences in the mean dates were significant (Appendix 6). However, there was no significant difference in the mean peak dates between the edges and the interiors (Appendix 6). The mean peak of flowers occurred between September 5th and 19th for all the environments except the south edge, where it occurred on October 6th (Appendix 4). We obtained the same result for unripe fruit, with mean peak dates ranging between October 18th and 28th for all the environments except the south edge, where it occurred on November 17th (Appendix 4). Ripe fruit peaked on November 6th on the east edge, but not until November 28th on the south edge (Appendix 4).

Microenvironmental conditions and phenological patterns

 The Principal Component Analysis (PCA) did not detect differences in the soil properties among the transects. Furthermore, soil features did not influence the intensity of *M. guianensis* phenophases (results not shown). According to the PCA, the east face experiences a higher incidence of photosynthetic active radiation (PAR), due to its cardinal orientation and to greater canopy openness (Fig. 5). Consequently, the temperature is higher and the air humidity is lower in the eastern transects. On the other hand, the southern transects present a more closed canopy, which results in a lower PAR incidence, a lower temperature and higher relative humidity (Fig. 5). The differences between the edge and the interior of each area were not as evident as the differences between the south and east edges. According to the increasing values of PAR and the temperature and the decreasing values of relative air humidity, we can establish a gradient of microenvironmental conditions starting on the south edge, followed by the south interior, then the east interior and, finally, the east edge.
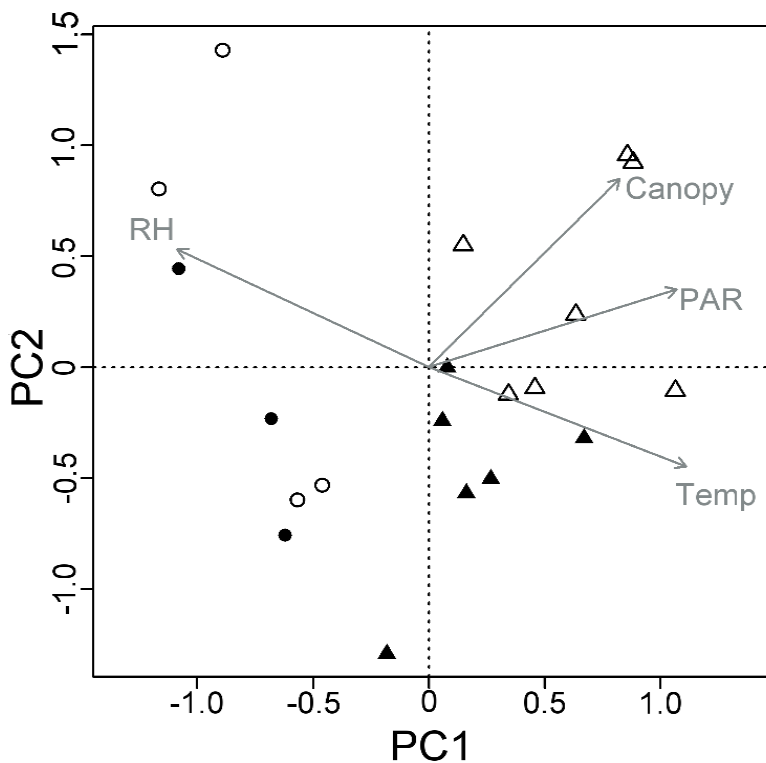
Fig. 5. Principal component analyses for transects distribution according to their microenvironmental characteristics. Variables measured: air temperature (Temp), air relative humidity (RH), incident photosynthetic active radiation (PAR) and canopy openness (Canopy). The first principal component explains 70% of data variation, while the second principal component explains 22% of data variation. Symbols indicate the localization of each transect in the cerrado study site: south edge (open circle), south interior (filled circle), east edge (open triangle) and east interior (filled triangle).

The first and second principal components explained about 70% and 22% of the data variation respectively (Table 3). According to the eigenvalues (Appendix 7), the first component summarizes the balanced effect of the four analyzed variables (temperature, relative humidity, canopy openness and PAR incidence) on the phenology. A higher value for the first component indicates higher PAR incidence and temperature and lower relative air humidity, whereas the second component presents the openness of the canopy as the dominant effect.

Microclimatic variables exhibited significant influences on *M. guianensis* phenology. We found statistically significant relationships between the mean intensity of the reproductive phenophases and the first principal component (Fig. 6). This component explained 59%, 61%, 60% and 58% of the variation of flower buds, flowers, unripe and ripe fruit respectively (Fig. 5). These analyses showed an ascending variation of the phenophase intensity as well as of the first component, starting on the south edge, followed by the south interior, the east interior and finally the east edge. On the other hand, there was no correlation between the first component and the vegetative phenophases, indicating a lack of influence of microenvironmental variations on leaf flush and leaf fall.
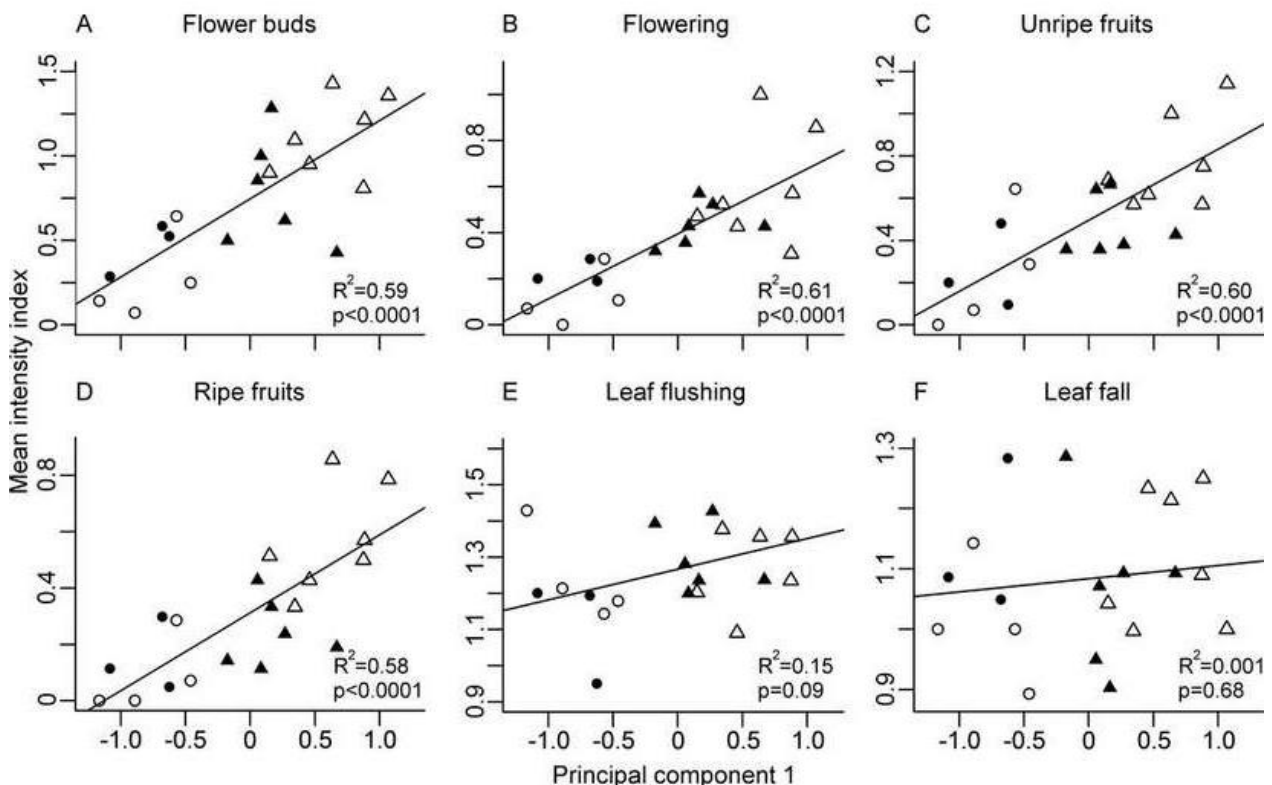
Fig. 6. Linear regressions between PCA's first principal component (PC1) of microenvironmental data and the average monthly intensity of reproductive and vegetative phenophases for the period between January 2005 and December 2011. Higher values of PC1 indicate environments with higher canopy openness, more incident photosynthetic active radiation, higher temperature and lower relative humidity. Determination index (R2) and p-value are provided for all linear regressions. Symbols indicate each environment of the cerrado study site: south edge (open circle), south interior (filled circle), east edge (open triangle) and east interior (filled triangle).

Discussion

Myrcia guianensis presented highly seasonal patterns, with vegetative and reproductive phenophases constrained by the seasonal climate. However, only the reproductive phenology was influenced by microclimate conditions. *M. guianensis* phenology differed between the edges and the interiors as well as between the south and east faces. Phenophase intensity and individual synchrony increased from the south edge to the south interior, east interior and east edge, following the gradient of microenvironmental conditions including increasing values of PAR and temperature and decreasing values of humidity. The flower and fruiting onset and peak occurred around 20 days earlier on the warmer and more illuminated east edge than on the south face.

The peak of leaf flush has been reported to be during the transition between dry and wet seasons for cerrado vegetation [38, 39]. Leaf fall peaked in the dry season, as has also been observed by other phenological studies in the cerrado [38, 39], probably as a defense mechanism against water loss and the death of individuals from water stress during drought [40]. The onset and peak of flower buds and anthesis in the dry season and of fruit in the wet season is an expected pattern in cerrado vegetation [38-41]. Flowering activity follows the first rain after the dry season, which is considered one of the main factors inducing flowering in tropical forests [39, 40] and cerrado environments [40]. Animal-dispersed species of cerrado vegetation usually fruit in the wet season, when water is available for the production of attractive fleshy fruit over a long period [13, 38-40]. The high synchrony of flowering and fruiting is also associated with greater attractiveness for pollinators and seed dispersers [42]. Other Myrtaceae phenological studies have posited that highly synchronous flowering and fruiting is a strategy to improve reproductive success [29, 30].

The differences in *Myrcia guianensis* reproductive phenology among the four environments were related to their microenvironmental conditions. The main differences were observed between the east and south faces. However, our results also indicate the influence of edge effects, mainly between the edge and the interior of the east face, where phenophase activity started earlier at the warmer edge. Phenophase intensity and individual synchrony increased from the south edge towards the south interior, the east interior and the east edge, following the gradient of microenvironmental conditions from more to less light and from warmer to cooler microclimatic conditions. In the same cerrado study site, individuals of pimenta-de-macaco (*Xylopia aromatica*) located on the east face presented with higher individual activity and synchrony [13]. Also, in the same cerrado area, angico-do-cerrado (*Anadenanthera peregrina*) trees on the edges and isolated in a pasture started flowering earlier than trees in the interior as a response to microclimatic conditions, mainly higher temperatures [21]. Zhao *et al.* [43] found a similar result for tropical species, where plants exposed to elevated temperatures flowered earlier, as predicted by photothermal models. Besides the temperature, different studies have observed a positive influence of light incidence on reproductive structures production [16, 44].

Since the synchrony and intensity of reproductive phenophases determine the attractiveness of plants for pollinators and seed dispersers, the observed changes in phenological patterns caused by edge effects and cardinal orientation may also affect plant-animal interactions and, consequently, the reproductive success of plants for which animals are pollen or seed vectors [3, 10, 45]. In addition, habitat loss has negative effects on pollinator abundance, resulting in lower pollen availability and fewer vectors to move pollen through the landscape [3, 46].

The different environments, possibly due to differences in microclimate conditions, particularly the higher temperature, influenced not only the synchrony and intensity of reproductive phenophases, but also the mean onset dates of flowering and fruit ripening, which occurred about one month earlier on the east edge. This result confirms the prediction based on extensive reviews of temperate species, phenological models and some warming experiments, which indicates earlier flower onset dates because of rising temperatures due to climate change [47, 48]. Therefore, the east face of our study site can be used to evaluate future warming impacts on tree phenology, as the highest temperatures and the lowest values of air humidity simulate future predictions of climate scenarios with warmer and dryer seasons [23]. Related to vegetative phenophases, we found a one-month delay in the leaf fall mean peak date on the east edge, which contrasts with the results found by Menzel *et al*. [47] that show a delayed autumn in warming experiments for temperate forests. The leaf flushing peak also occurred almost one month earlier on the east edge and around 15 days earlier in the east interior than on the south face, which is consistent with the advanced leafing phenology observed through warming experiments [48].

The differences in flowering and fruiting between the east and south edges may indicate a combined influence of edge effects and orientation, as both promote a wetter microenvironment with less light at the south edge. Besides the orientation and its position in relation to the sun, the south edge presents structural variations that contribute to the shaded environment. These structural characteristics include denser vegetation cover, a higher proportion of woody species [24], and a higher number of lianas (woody vines) (Camargo *et al. under review*). Therefore, the reported phenological differences as well as the structural differences between environments are a response to environmental conditions related to cardinal orientation and edge effects [24, 49].

Implications for conservation

We showed that microenvironmental variations related to edges and cardinal orientation influence plant phenological patterns in the cerrado, with changes found in onset dates, individual synchrony and the intensity of reproductive phenophases, mainly due to temperature. Leaf changes are more constrained by the macroclimate, presenting a more regular pattern within environments with different microenvironmental conditions. For plant communities' conservation, it is important to consider that changes in the intensity and synchrony of flower and fruit production over time may affect plant-animal interactions, with consequences for pollination and seed dispersal success [46, 47]. We suggest that the warmer and more illuminated east face could be used to evaluate plant phenology responses to future climate change scenarios [21, 23]. Moreover, given the high number of lianas (woody vines) on the south edge, our study provides an example of how changes in the vegetation structure and composition may influence phenological patterns and limit flower and fruit production.

Acknowledgements

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Appendices
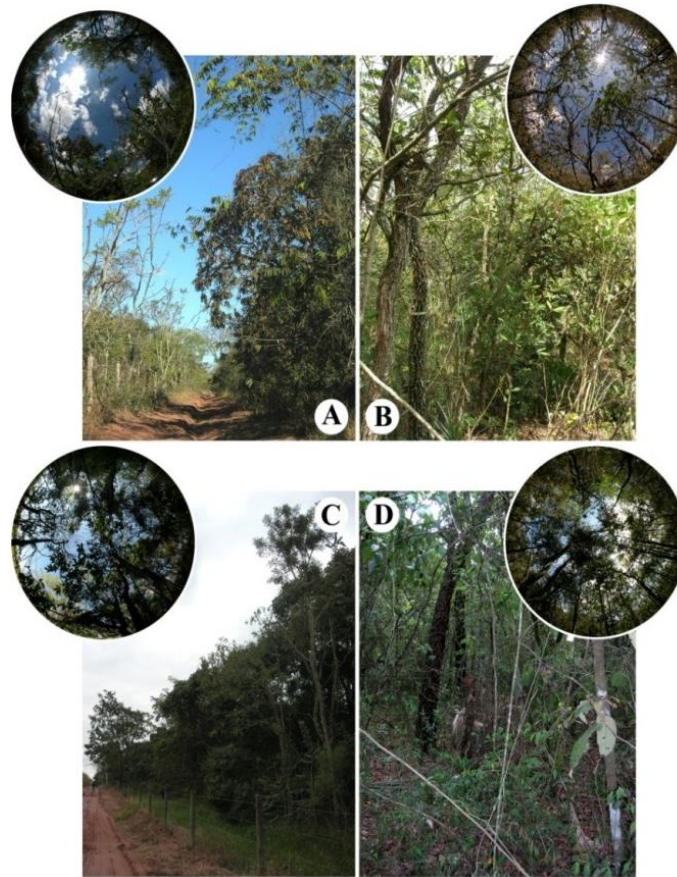
Appendix 1. Aspects of the vegetation in the east edge (EE), east interior (EI), south edge (ES) and south interior (SI) environments of the cerrado study site, southeastern Brazil. In detail, hemispheric photographs showing the canopy openness. Pictures: M. G. G. Camargo.

Appendix 2. Vegetative and reproductive phenophases of *Myrcia guianensis* (Myrtaceae). A) Leaf flush and developing leaves; B) Flower buds and flowers; C) Flowers and fewer flower buds; D) Unripe (reddish) and ripe (black) fruits, with a detail of ripe fruits and seeds (scale = 1cm). Pictures: M. G. G. Camargo.
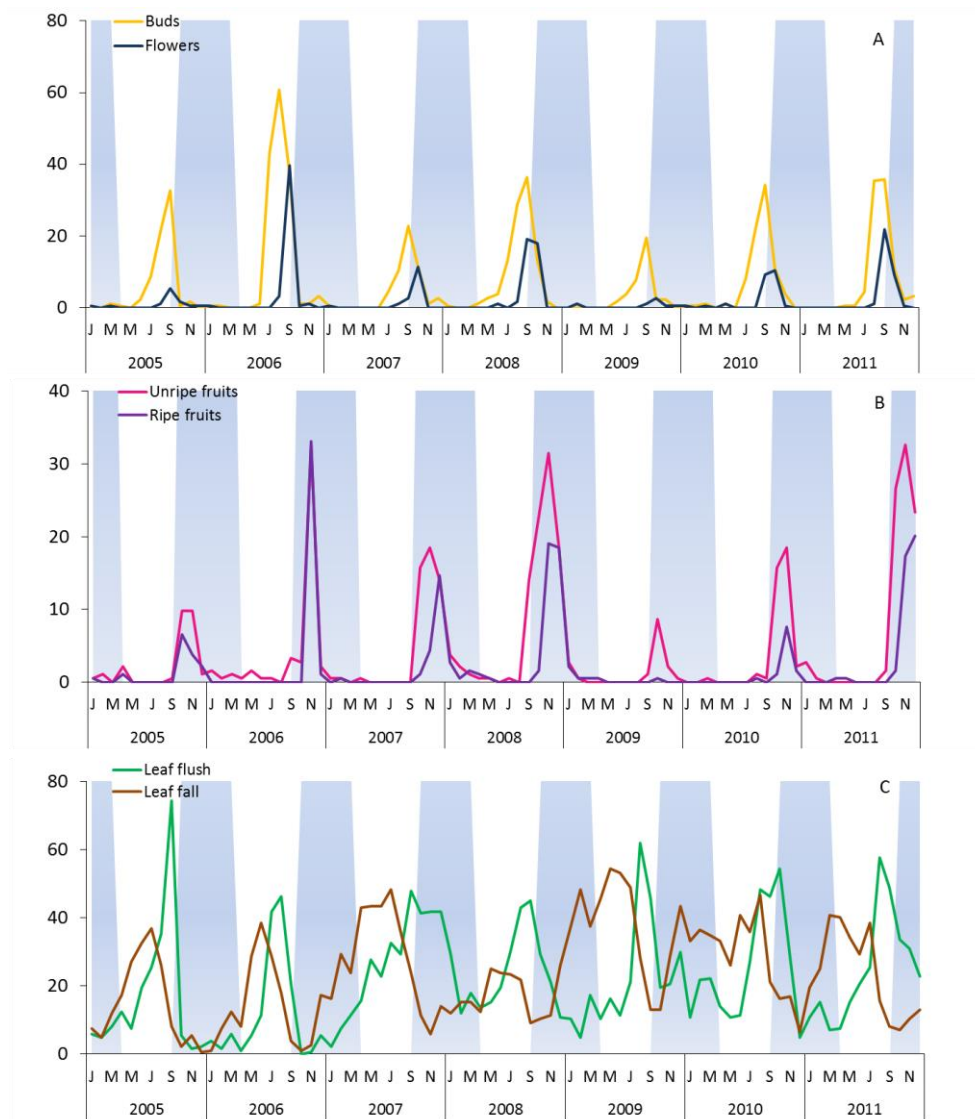
Appendix 3. Monthly intensity of flowering (A), fruiting (B) and leaf changes (C) from January 2005 to December 2011 in the individuals of *Myrcia guianensis* sampled in a cerrado study site, southeastern Brazil. The blue area indicates the wet season.

Appendix 4. Circular statistics of flowering and fruiting onset and peak dates based on the mean pattern from January 2005 to December 2011 for *Myrcia guianensis* individu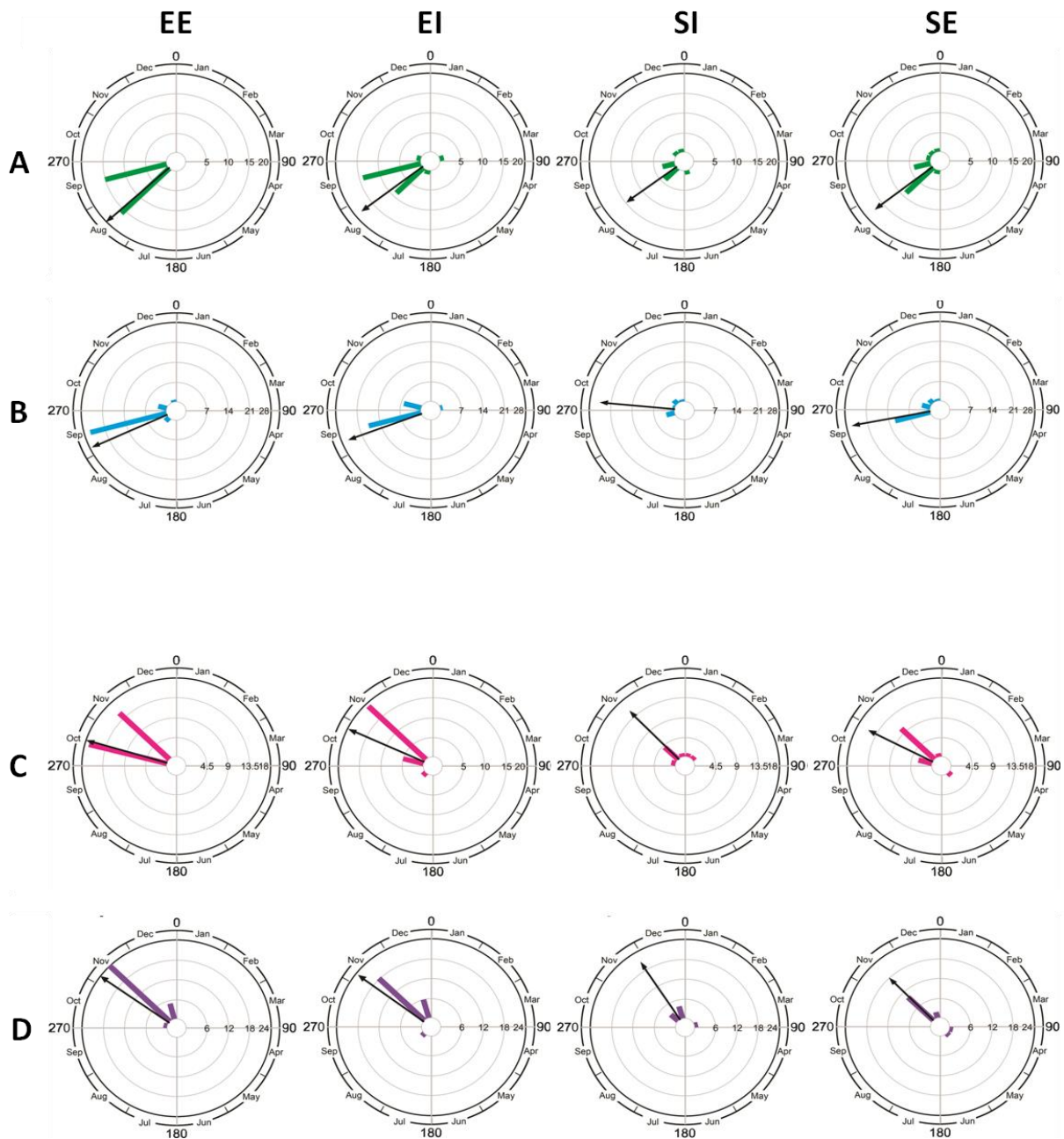als sampled in the east edge (EE), east interior (EI), south edge (ES) and south interior (SI) of the cerrado study site and the corresponding mean angles, mean dates and vector r.

ONSET	Subgroup	Number of observations	Mean vector (μ)	Mean date	Length of mean vector (r)	Rayleigh test (Z)	Rayleigh test (p)
Flower bud	EE	32	181.476°	3rd July	0.94	28.402	<0.001
	EI	25	182.736°	4th July	0.82	17.275	<0.001
	SE	7	205.666°	27th July	0.67	4.48	0.008
	SI	18	193.629°	15th July	0.77	10.694	<0.001
Flower	EE	32	233.571°	24th August	0.99	31.242	<0.001
	EI	24	240°	31th August	0.9	20.163	<0.001
	SE	7	256.102°	16th September	0.9	5.7	<0.001
	SI	13	250.019°	10th September	0.88	14.017	<0.001
Unripe fruit	EE	29	257.771°	18th September	0.97	30.109	<0.001
	EI	14	261.683°	22th September	0.94	22.163	<0.001
	SE	5	282.111°	13th October	0.82	5.422	0.002
	SI	8	276.896°	7th October	0.77	8.828	<0.001
Ripe fruit	EE	30	290.012°	21th October	0.97	28.346	<0.001
	EI	22	302.497°	2nd November	0.93	21.556	<0.001
	SE	5	325.666°	26th November	0.84	5.6	0.001
	SI	13	299.25°	30th October	0.74	7.653	<0.001

PEAK	Subgroup	Number of observations	Mean vector (μ)	Mean date	Length of mean vector (r)	Rayleigh test (Z)	Rayleigh test (p)
Flower bud	EE	32	227.458°	18th August	0.97	29.374	<0.001
	EI	26	231.918°	23th August	0.89	20.456	<0.001
	SE	10	232.797°	24th August	0.71	5.07	0.004
	SI	16	231.499°	22th August	0.84	12.07	<0.001
Flower	EE	31	245.293°	5th September	0.95	28.669	<0.001
	EI	23	249.033°	9th September	0.9	20.081	<0.001
	SE	7	275.846°	6th October	0.85	5.076	0.002
	SI	13	258.812°	19th September	0.91	14.823	<0.001
Unripe fruit	EE	29	287.357°	18th October	0.97	30.11	<0.001
	EI	14	295.26°	26th October	0.96	23.045	<0.001
	SE	3	316.669°	17th November	0.81	5.29	0.002
	SI	7	297.715°	28th October	0.84	10.483	<0.001
Ripe fruit	EE	29	306.475°	6th November	0.97	28.445	<0.001
	EI	21	307.499°	7th November	0.94	22.127	<0.001
	SE	4	327.787°	28th November	0.84	5.616	0.001
	SI	13	316.076°	16th November	0.72	7.272	<0.001

Appendix 5. Circular distribution of peak dates for flower buds (A), flowers (B), unripe fruits (C) and ripe fruits (D), based on the mean pattern from January 2005 to December 2011 for *Myrcia guianensis* individuals sampled in the east edge (EE), east interior (EI), south edge (ES) and south interior (SI) of the cerrado study site. All mean angles are significant (Rayleigh test, p<0.001) and are represented by the arrows, while vector r (0 to 1) indicates the concentration around the mean angle.

Appendix 6. Values of Watson-Williams test (Z) for the comparison of the onset and peak mean angles of reproductive phenophases between the east edge (EE), east interior (EI), south edge (ES) and south interior (SI) environments of the cerrado study site.

ONSET	SE X SI		EE X EI		EE X SE		EE X SI		SE X EI		EI X SI	
	Z	p value	Z	p value	Z	p value	Z	p value	Z	p value	Z	p value
Flower bud	0.39	n.s.	0.03	n.s.	3.75	n.s.	1.7	n.s.	1.86	n.s.	0.77	n.s.
Flower	0.21	n.s.	1.32	n.s.	10.15	0,003	7.09	0,011	1.74	n.s.	1.22	n.s.
Unripe fruit	0.08	n.s.	0.58	n.s.	6.84	0,013	4.51	0,039	3.31	n.s.	2.09	n.s.
Ripe fruit	1.90	n.s.	5.20	0,000	15.13	0,027	0.9	n.s.	4.04	n.s.	0.08	n.s.

PEAK	SE X SI		EE X EI		EE X SE		EE X SI		SE X EI		EI X SI	
	Z	p value	Z	p value	Z	p value	Z	p value	Z	p value	Z	p value
Flower bud	0.01	n.s.	0.61	n.s.	0.28	n.s.	0.33	n.s.	0.004	n.s.	0.002	n.s.
Flower	1.76	n.s.	0.37	n.s.	9.87	0,03	4.40	0,041	4.55	0,041	1.42	n.s.
Unripe fruit	1.38	n.s.	3.71	n.s.	11.24	0,02	2.02	n.s.	4.66	0,039	0.09	n.s.
Ripe fruit	0.37	n.s.	0.05	n.s.	6.73	0,014	1.01	n.s.	3.85	n.s.	0.59	n.s.

Appendix 7. Eigenvalue and eigenvectors of the principal component analyses applied to the microenvironmental variables (air temperature, relative humidity, incident photosynthetic active radiation and canopy openness). The first and second components together explain 92% of data variation.

	PC1	PC2	PC3	PC4
Eigenvalue	2.81	0.88	0.25	0.06
Explained proportion	0.7	0.22	0.06	0.01
Cumulative proportion	0.7	0.92	0.98	1
Eigenvectors:				
Temperature	0.54	-0.4	-0.3	0.7
Relative humidity	-0.5	0.46	0.12	0.7
Photosynthetic active radiation	0.52	0.3	0.8	0.06
Canopy	0.4	0.74	-0.5	-0.1