



Seasonal and vertical distribution of floral resources and its implications for the conservation of pollinators

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ABSTRACT

The diversity of plant species in blooming throughout the year is a way of ensuring the presence of floral resources, as the spatiotemporal distribution of these resources assists in the movement of pollinators and guarantees local ecosystem services. The aim of this study was to describe the seasonal variations in the vertical distribution of the floral resources that keep the pollinators in Cerrado areas, the savanna region in Central Brazil, a biodiversity hotspot that depends more than 80% on bees for pollination. We studied four cerrado *stricto sensu* areas and evaluated monthly the flowering phenology, taking into account the number of individuals for each plant species blooming in all vertical strata (arboreal, shrubby, herbaceous, and lianas) and main floral resources (nectar, pollen, and floral oil). We evaluated the annual distribution of flowering plant species and individuals, and the availability of floral resources. We found a seasonal flowering pattern for the whole cerrado *stricto sensu*, with differences between areas, strata and floral resources types. The floral resources varied idiosyncratically among the strata over time, suggesting complementary blooming patterns throughout the year. The shrubby, herbaceous and liana species were key determinants in the availability of floral resources through the seasons. Our results reinforce the importance of including all the strata in plant surveys, as well as highlight the importance of the vertical stratification in the Cerrado plant formations as a source of floral resources during the time in which there are fewer resources available for pollinators in surrounding forest areas.

1. Introduction

The diversity of plant species in blooming throughout the year is a way to ensure the availability of floral resources, as the spatiotemporal distribution of these resources assists in the movement of pollinators and guarantees local ecosystem services (Hadley and Betts, 2012; Kremen et al., 2007). Understanding the flowering phenology is essential to the conservation of pollinators, and therefore to the conservation of the plants themselves, as more than 90% of flowering plants depend on pollinators for their reproduction (Potts et al., 2010). Bees are the most important pollinators in natural (Bawa et al., 1985; Oliveira and Gibbs,

2000; Silva et al., 2012), agricultural (Freitas et al., 2014; Garibaldi et al., 2013; Wolowski et al., 2019; Silva et al., 2020), and urban ecosystems (Aleixo et al., 2014; Silva et al., 2017; Silva and Kleinert, 2020b). Flowering plants have a strong influence on the distribution and life of bees, as these plants offer pollen, nectar, and floral oils for their survival (Michener, 2007).

In the Cerrado, the Neotropical savanna region in Central Brazil, more than 80% of the plant species depend directly or indirectly on bees for pollination (Silberbauer-Gotsberger and Gotsberger, 1988). Silva et al. (2012) found an even higher percentage of plant species pollinated exclusively or mainly by bees (from 85.4% to 93.8%) when compared to

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other studies in the Cerrado (Silberbauer-Gotsberger and Gotsberger, 1988; Oliveira and Gibbs, 2000; Martins and Batalha, 2007). The authors attributed this to the fact that they included flowering plants from all vertical strata in the studied areas, while most of previous studies only included species from one or another stratum and often excluded entire groups of plants, such as lianas.

The Cerrado is a biodiversity hotspot (Myers et al., 2000) which consists of complex plant formations ranging from forests - such as gallery forests, dry forests, and cerrado woodlands - to savanna formations - cerrado *stricto sensu*, grassland, dry and wet grasslands, and palm swamp (Mendonça et al., 1998; Ribeiro and Walter, 2008). However, the most characteristic formations are typical savannas (cerrado *stricto sensu*) with trees, shrubs and even lianas embedded into a more or less continuous herbaceous and grass layer/stratum (Ribeiro and Walter, 2008). Unlike denser vegetation, such as tropical forests, where plants pollinated by bees belongs to the higher strata (Bawa et al., 1985; Bawa, 1990; Kress and Beach, 1994; Yamamoto et al., 2007), Silva et al. (2012) found that many species in the herbaceous stratum of the savannas also depend on bees to pollination, thus evincing the importance of these plants to attract and maintain of the pollinator's community.

The Cerrado region has a high richness of bees, ranging from 51-196 species only in cerrado *stricto sensu* plant formations (Anacleto and Marchini, 2005; Andena et al., 2005; Carvalho and Bego, 1996; Santos et al., 2004). The flowering phenology in Cerrado can be determined not only by environmental constraints (as it occurs in tropical seasonal climate with a marked dry season), but also by other factors such as nutrients available in the soil and frequent fires, and the interaction among them (Oliveira, 2008), and these phenological dynamics directly affect the availability of resources for floral visitors and/or pollinators.

Although there are seasonal bee species in the Cerrado, most of them can visit flowers and build nests throughout the year, including the cooler part of the dry season (Carvalho and Bego, 1996). Therefore, the demand for food by bees is high, and there is a need for the presence of blooming species throughout the seasons. However, there are no published studies regarding the phenological dynamics on the vertical strata that comprise herbs, shrubs, trees, and lianas within a single type of plant formation.

The vertical stratification is important for maintaining diversity of

pollination systems in general and for the diversity of bees in particular (Silva et al., 2012). Plants of the tree stratum present flowering peaks at the beginning of the rainy season, while the species of the other strata bloom at different times throughout the year (Oliveira and Gibbs, 2000; Batalha and Martins, 2004). The heterogeneous distribution of pollination systems within the vertical stratification can generate a mosaic in the availability of floral resources used by pollinators, which can be as important as the horizontal mosaics (Silva et al., 2012) for the maintenance of their communities in the Cerrado. Therefore, we hypothesize that if we include all the strata to evaluate the floral resources availability, we can find different patterns in the floral resources distribution than those showed in the literature. In this context, we aimed to answer: Do different vertical strata show different phenological patterns in relation to seasonality? What are the implications for this stratification to the maintenance of pollinator communities? We expect to find phenological differences between strata and a significant contribution of the lower strata, such as shrubs and herbs, in the maintenance of food to pollinators communities.

2. Material and methods

2.1. Study areas

We studied four Cerrado areas in the Triângulo Mineiro region in Minas Gerais, Brazil (Fig. 1), where we selected transects through cerrado *stricto sensu* plant formations (Silva et al., 2012). Area 1 has 60 ha, was located in the municipality of Uberlândia (778581.00 m E; 7886223.00 m S) and is formed by cerrado vegetation (woodland), cerrado *stricto sensu*, and forest gallery, inside the Experimental Água Limpa Farm Federal University of Uberlândia. Area 2, with 23 ha, was located in the municipality of Araguari (805225.15 m E; 7929905.73 m S) and is a Private Natural Reserve inside Campo Alegre farm. It includes both cerrado and cerrado *stricto sensu* plant formations. Area 3, of 127 ha, corresponded to the Natural Reserve of the Clube de Caça e Pesca de Itororó (CCPIU), located in Uberlândia (783652.00 m E; 7897442.00 m S). The vegetation is composed predominantly by cerrado *stricto sensu* and a long Vereda palm swamp. Area 4 belonged to Estação Ecológica do Panga, located in the southern region of Uberlândia (774150.00 m E;

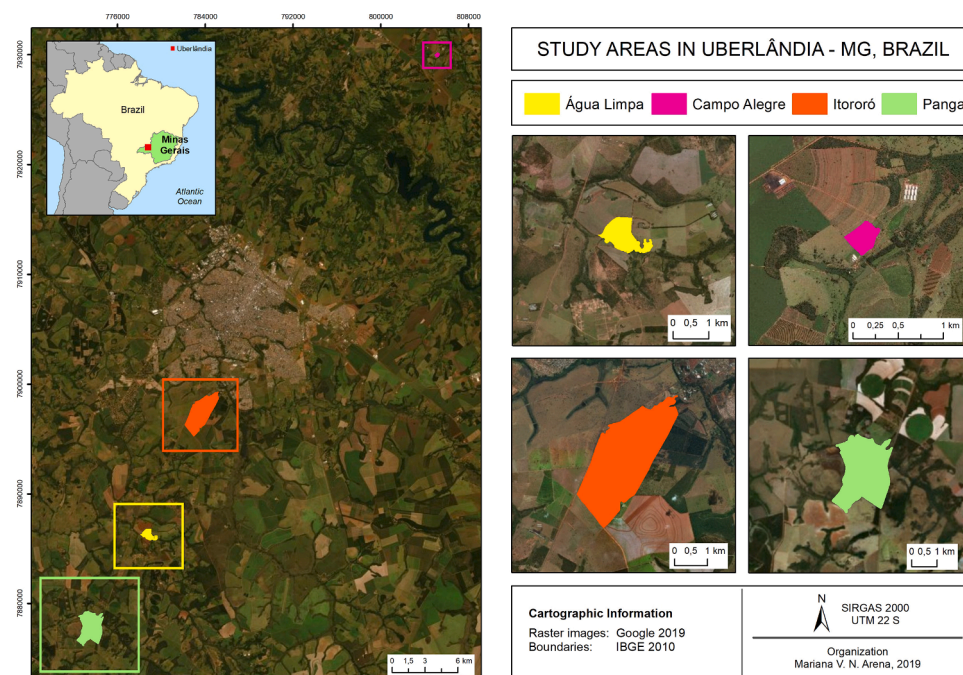


Fig. 1. Study areas in cerrado *stricto sensu* from January 2006 to December 2007. Area 1: “Água Limpa” Experimental Farm of the Federal University of Uberlândia; Area 2: “Campo Alegre” Farm; Area 3: Reserve of the “Clube de Caça e Pesca de Itororó”; Area 4: Ecological Station of Panga.

7876666.00 m S) with 409.5 ha. The vegetation in this area includes cerrado *stricto sensu*, Vereda palm swamps, semi-deciduous forest and gallery forests (Schiavini and Araújo, 1989).

The climate of the region is Aw, according to the Köppen (1948) classification, with two well defined seasons, a warmer and humid from October to March (rainy season), and a cooler and dry season from April to September (dry season). The average temperature was 23°C (between 9 and 37°C in the two studied years). The average rainfall accumulated per year was 491 mm (supplementary material, Figure 1).

2.2. Flowering phenology and seasonal distribution of floral resources

For the flowering phenology data, we used the floristic composition survey from Silva et al. (2012). These authors studied the floristic composition of the four cerrado *stricto sensu* plant formation, in which found a highest similarity index between Area 1 and 4 (0.6484), and the lowest between Area 2 and 3 (0.5472) (supplementary material, Figure 2). From January 2006 to December 2007, we evaluated the monthly flowering phenology in all the studied areas by walking 1000 m transects and recording all blooming individuals within a distance of up to 10 m on each side, a total of 2 ha for each of the studied areas. We counted the number of individual flowering plants and classified each plant species according to their main floral resource available to pollinators, based on field observations and analyses (N = nectar, P = pollen, O = floral oil). If the plant species provided two kinds of resources in the same flower (NP, PO), we included them with those that provided each kind of resource (N, P or O), so that they were often counted twice in the analyses.

To obtain more details on the available floral resource, we collected flowers and took them to the laboratory in order to evaluate the presence of secretory structures. We also revised the literature for additional information on their floral and reproductive biology. We considered plant species of all vertical strata, which were classified according to habit or life form as (i) arboreal, (ii) shrubby, (iii) herbaceous, and (iv) liana (see also Silva et al., 2012) (supplementary material, Table 1). To classify the plants per strata, we considered the woody individuals with circumference at breast height (CBH) >15 cm and more than 2 m as arboreal; the woody individuals with stem between 1 and 2 m in height and CBH <15 as shrubby; non-woody individuals with stem <1 m tall as herbaceous; and woody individuals which develop supported on other plants as lianas. To count the number of shrubby and herbaceous plants we considered each clump as an individual (Bernacci and Leitão Filho, 1996; Rizzini and Rizzini, 1983; Silva et al., 2012).

We identified the plant species *in loco* whenever possible but collected and sent them to specialists whenever necessary. We used the Angiosperm Phylogeny Group (APG III) (Chase and Reveal, 2009) to classify the Botanical families, and the exsiccates were deposited in the Herbarium Uberlandense of the Federal University of Uberlândia.

2.3. Data analyses

To analyze the ecological parameters of each area we used the diversity index of Shannon (H') (Shannon, 1948), the evenness index of Pielou (J') (Pielou, 1966), and the dominance index of Berger-Parker (D) (Magurran, 2004). For the phenological study we used the Rayleigh test of uniformity (Z) for circular distributions with a significance level of 5% to evaluate (i) the seasonal distribution of flowering plant species in the study areas; (ii) the seasonal distribution of flowering plant species in each stratum; and (iii) the seasonal distribution of flowering plant individuals for each floral resource attractive for pollinators (Morellato et al., 2000). We used the chi-square test (χ^2) according to Batschelet (1981) to assess whether the phenological patterns were similar between the years of study, among the study areas and among the vegetation strata. We also used the chi-square test to check whether types of floral resources differed among strata. To calculate the circular statistical parameters, the months were converted into angles with intervals

of 30°, starting in 0° to 30°, corresponding January, and ending at 330° to 360°, which corresponded to December. We used the average date and concentration (r) of flowering events to calculate this transformation. The vector of the histogram indicates the average angle, which corresponds to the average date of occurrence of the event (concentration of the event around them). We tested the hypotheses: H_0 = plant individuals providing floral resources were uniformly distributed throughout the year, and therefore there was no seasonality; and H_1 = plant individuals providing floral resources were unevenly distributed throughout the year, and therefore there was seasonality. If H_1 was corroborated, the intensity of flowering concentration around an average date, denoted by r , could be considered a measurement of the degree of seasonality. The value of r ranges from 0 (flowering uniformly distributed throughout the year) to 1 (flowering concentrated on a single month), as described by Morellato et al. (2000).

3. Results

We found 178 plant species from 114 genera and 41 botanical families (supplementary material, Table 1). In general, the botanical families with the highest species representativity, were well represented in the four areas studied, in decreasing order for Fabaceae ($n = 32$), Asteraceae ($n = 17$), Malpighiaceae ($n = 16$), Myrtaceae ($n = 15$) and Bignoniaceae ($n = 14$) (supplementary material, Table 2). Regarding all studied areas, the flowering phenology showed a significant flowering concentration ($r = 0.126$, $Z = 11.082$, $p = 0.001$), and a seasonal blooming pattern during the two years survey. The period with more blooming species varied between the two survey years, and was lower in 2006 ($r_{2006} = 0.079$, $Z = 4.014$, $p < 0.05$; $r_{2007} = 0.177$, $Z = 23.148$, $p < 0.001$) (supplementary material, Figure 3).

Concerning each area separately, Area 3 was the most species rich with 115 plant species, followed by Area 2 (97). We found differences in the diversity (Area 1 = 3.378; Area 2 = 2.960; Area 3 = 3.173; Area 4 = 3.455), evenness (Area 1 = 0.747; Area 2 = 0.647; Area 3 = 0.668; Area 4 = 0.767), and dominance (Area 1 = 0.147; Area 2 = 0.281; Area 3 = 0.211; Area 4 = 0.109) among them. The phenological patterns varied among the areas, showing significant differences between areas 1 and 3 ($\chi^2 = 21.35$; $p = 0.03$) and areas 2 and 3 ($\chi^2 = 22.63$; $p = 0.02$) (supplementary material, Table 3). We also observed species blooming throughout the years, except in December (Area 1) and November (Area 2) in 2006 (Fig. 2 A-B and Table 1). In 2006 only Area 4 ($r = 0.15$; $p = 0.029$) showed an effect of seasonality on the flowering period, whereas in the other areas there was a higher uniformity (Table 1). In 2007 we verified the opposite, since Area 4 showed uniformity in the distribution of blooming species ($r = 0.884$; $p = 0.413$), unlike the other areas (Table 1). When we observed the phenological patterns of each area between the years, we found that Areas 1 and 2 presented significant differences ($\chi^2_{\text{Area 1}} = 11.411$, $p = 0.001$; $\chi^2_{\text{Area 2}} = 4.672$, $p = 0.031$). Regarding the individuals in flower throughout the years, we found variation among areas (Fig. 2 C-D), and all of them presented seasonality (Table 1). In 2006, the average angles were distributed from June to October, while in 2007 all areas presented the average angles in November (Table 1). All areas presented a significant difference in the phenological patterns between years (Table 1).

Taking into account the vertical stratification, we verified that the arboreal ($r = 0.24$ and $p < 0.001$ in 2006; $r = 0.38$ and $p < 0.001$ in 2007) and shrubby ($r = 0.13$ and $p = 0.007$ in 2006; $r = 0.18$ and $p < 0.001$ in 2007) strata presented seasonality in both years. Herbaceous species presented seasonality only in the first year ($r = 0.37$; $p = 0.002$), and lianas and epiphytes were more evenly distributed throughout the study period ($r = 0.09$ and $p = 0.713$ in 2006; $r = 0.28$ and $p = 0.119$ in 2007) (supplementary material, Figure 4 and Table 4). We observed that species in the arboreal stratum showed the highest number of species in bloom during the rainy season (from October to December), whereas the number of flowering shrub species were highest during the dry season (from April to September; supplementary material, Figure 4). Moreover,

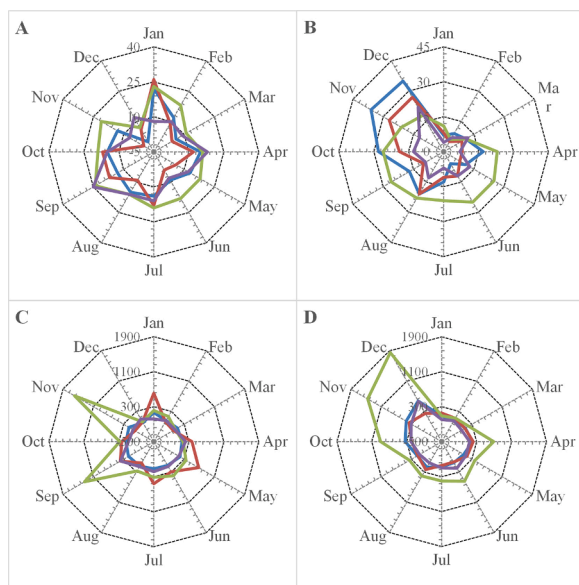


Fig. 2. Circular diagrams of the distribution of floral resources used by pollinators in cerrado *stricto sensu*, represented by the number of species (A and B) and individuals (C and D) blooming in the study areas throughout the two years of survey, 2006 (A and C) and 2007 (B and D). The lines show the total of blooming species (A and B) and individuals (C and D) in each month - blue lines represent Area 1, red lines Area 2, green lines Area 3, and purple lines Area 4. The months of the year are represented in 360°, in a way that each month period is comprised in a 30° interval - starting from 0° to 30° in January and ending in 360° in December. Concentric circles represent the scale marks of the circular axis.

we found that the flowering patterns varied between years for most strata (except for liana) and between strata, suggesting complementarity between the strata in the study period (supplementary material, Table 4).

In general, the main floral resources used by pollinators (nectar, pollen, and floral oil) were available throughout both years (supplementary material, Figure 5 and Table 5), showing a seasonal pattern in the distribution of each floral resource ($r = 0.12$ for nectar; $r = 0.22$ for pollen; $r = 0.52$ for oil; $p < 0.001$ for all resources). We observed a greater concentration of floral resources availability during the first months of the raining season (October to December). The peak of individuals providing nectar and pollen varied between years, but the peak of individuals with oil flowers was always higher in November (supplementary material, Figure 5). The periods when floral resources were available most abundantly varied between strata so that blooming patterns among them were complementary and resources available throughout the year (supplementary material, Figure 6 and Table 6). There was also a variation on the average period of floral resources availability in different strata between years. In general, pollen and nectar were the most abundant floral resources in all strata, especially in arboreal and shrubby strata (supplementary material, Figure 6 and Table 6).

We found a vertical stratification in the floral resources' distribution in the studied areas and significant differences among the strata (supplementary material, Table 7). This stratification was even more evident when we analyzed the distribution of the floral resources in the strata within the same area (Fig. 3–6; Tables 2–5). In all areas, the arboreal and shrubby strata contributed significantly to the availability of flower resources. However, the herbaceous and liana strata provided pollen and nectar during periods of the year when this resource was scarce, contributing to the food supply for pollinators, even though these strata had low representation throughout the year (Figs. 3–6; Tables 2–5).

In Area 1, the peak of blooming individuals in the arboreal stratum

Table 1

Descriptive statistics, uniformity analysis of phenology (Rayleigh test of uniformity - Z) applied to the circular distribution of plant species in blooming per stratum in cerrado *stricto sensu* areas from January 2006 to December 2007, and comparison of phenological patterns between years (Chi-Squared (χ^2) test) for the four strata.

	Area 1 Blooming species 2006	Area 2	Area 3	Area 4
Observation (N)	147	128	210	156
Average angle (a)	222.46	286.102	244.663	224.67
	August	October	September	August
Concentration (r)	0.046	0.095	0.065	0.151
Test of Rayleigh (Z)	0.307	1.163	0.899	3.556
Uniformity (p)	0.736	0.312	0.407	0.029
2007				
Observation (N)	211	165	236	131
Average angle (a)	302.344	291.682	218.512	292.911
	November	October	August	October
Concentration (r)	0.293	0.27	0.188	0.082
Test of Rayleigh (Z)	18.118	12.071	8.367	0.884
Uniformity (p)	< 0.001	< 0.001	< 0.001	0.413
Chi-Squared test (χ^2)	$\chi^2 = 11.441$	$\chi^2 = 4.672$	$\chi^2 = 1.516$	$\chi^2 = 2.178$
p value	$p < 0.001$	$p = 0.031$	$p = 0.218$	$p = 0.140$
Blooming individuals				
2006				
Observation (N)	1539	3165	5178	1633
Average angle (a)	187.851	155.692	271.158	202.051
	July	June	October	July
Concentration (r)	0.114	0.268	0.433	0.326
Test of Rayleigh (Z)	19.977	226.645	968.935	173.534
Uniformity (p)	< 0.001	< 0.001	< 0.001	< 0.001
2007				
Observation (N)	2373	2023	7406	1889
Average angle (a)	320.067	327.357	312.075	316.421
	November	November	November	November
Concentration (r)	0.401	0.209	0.316	0.28
Test of Rayleigh (Z)	382.086	88.546	741.79	147.921
Uniformity (p)	< 0.001	< 0.001	< 0.001	< 0.001
Chi-Squared test (χ^2)	$\chi^2 = 767.343$	$\chi^2 = 1936.436$	$\chi^2 = 2893.345$	$\chi^2 = 853.749$
p value	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$

corresponded to the massive flowering of *Matayba guianensis* Aubl (Sapindaceae), which provided nectar and pollen. *Solanum lycocarpum* A. St. Hil. (Solanaceae) also contributed to the availability of pollen in this stratum, and *Byrsonima coccolobifolia* Kunth (Malpighiaceae) with floral oil. In the shrubby stratum, the blooming peak occurred because of the massive flowering of *Byrsonima intermedia* A. Juss., which provided pollen and floral oil. Among the nectar sources, *Zeyheria montana* Mart. (Bignoniaceae), *Adenocalymma campicola* (Pilg.) L. Lohmann (Bignoniaceae), and *Bauhinia brevipes* Vog. (Fabaceae) were responsible for the peak of the blooming individuals in this stratum. *Trichogonia attenuata* G. M. Barroso and *Vernonia fruticulosa* (Mart.) DC. (Asteraceae) were important sources of nectar and pollen in the herbaceous stratum. Among the lianas, *Fridericia florida* (DC.) L. Lohmann (Bignoniaceae) and *Serjania reticulata* Cambess. (Sapindaceae) provided mainly nectar (but also some pollen), while *Heteropteris anoptera* A. Juss (Malpighiaceae) was the only floral oil plus pollen source (supplementary material, Table 1).

In Area 2, the blooming peak in the arboreal stratum was due also to the massive flowering of *M. guianensis* and *S. lycocarpum*, which provided nectar plus pollen and pollen, respectively. Among trees,

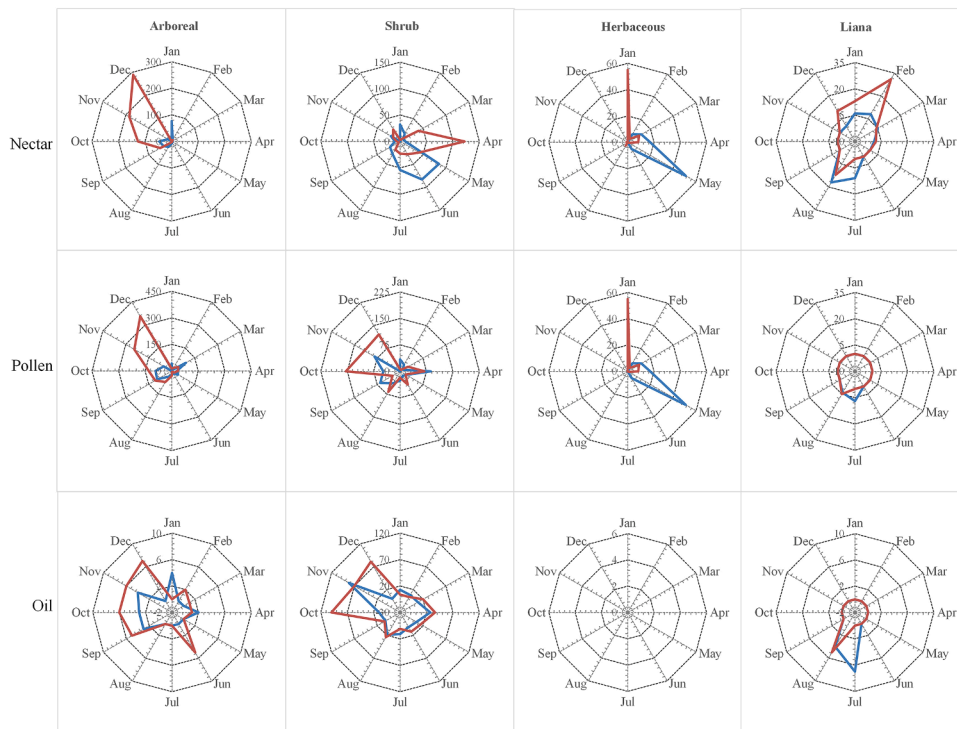


Fig. 3. Circular diagrams of the distribution of floral resources used by pollinators in the vertical strata in cerrado *stricto sensu*, represented by the number of blooming individuals in the Area 1 throughout the two years of survey. The lines show the total of blooming individuals in each month - blue lines represent the year of 2006 and red lines the year of 2007. The months of the year are represented in 360°, in a way that each month period is comprised in a 30° interval - starting from 0° to 30° in January and ending in 360° in December. Concentric circles represent the scale marks of the circular axis.

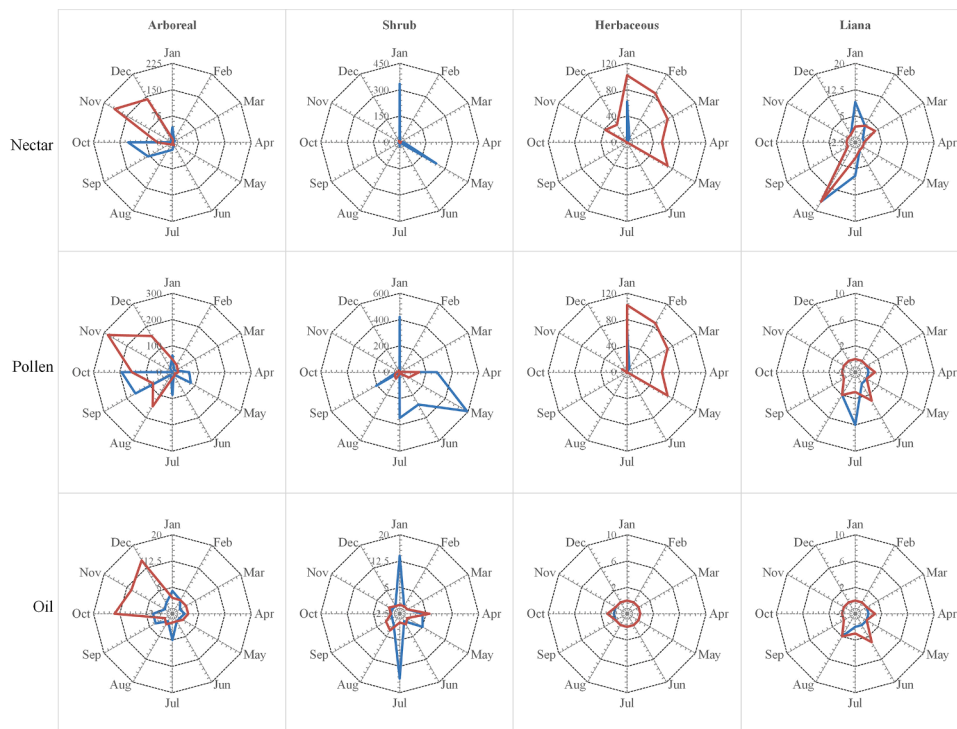


Fig. 4. Circular diagrams of the distribution of floral resources used by pollinators in the vertical strata in cerrado *stricto sensu*, represented by the number of blooming individuals in the Area 2 throughout the two years of survey. The lines show the total of blooming individuals in each month - blue lines represent the year of 2006 and red lines the year of 2007. The months of the year are represented in 360°, in a way that each month period is comprised in a 30° interval - starting from 0° to 30° in January and ending in 360° in December. Concentric circles represent the scale marks of the circular axis.

Byrsonima coriacea (Sw.) Kunth also contributed to pollen and floral oil availability. In the shrubby stratum *Eugenia calycina* Cambess. (Myrtaceae) and *Rhynchanthera grandiflora* (Aubl.) DC. (Melastomataceae) contributed most to the pollen availability during the blooming peak. *Vernonia polyanthes* Less. and *Ageratum fastigiatum* (Gardn.) R.M.King H. Rob. (Asteraceae) were important nectar and pollen sources among the shrubs. *Heteropteris byrsonimifolia* A. Juss., *Peixotoa tomentosa* A. Juss. (Malpighiaceae), and *Heteropteris escalloniifolia* A. Juss. shrubs were

important pollen and mainly floral oil providers. *Vernonia scabra* (Pers.) was the most representative species providing nectar and pollen in the herbaceous strata. *Serjania reticulata* was responsible for the peak of blooming lianas providing nectar plus pollen while *H. anoptera* was the only floral oil plus pollen source in this stratum (supplementary material, Table 1).

Matayba guianensis was also the most representative tree in Area 3, responsible for the peak of blooming individuals in the arboreal stratum,

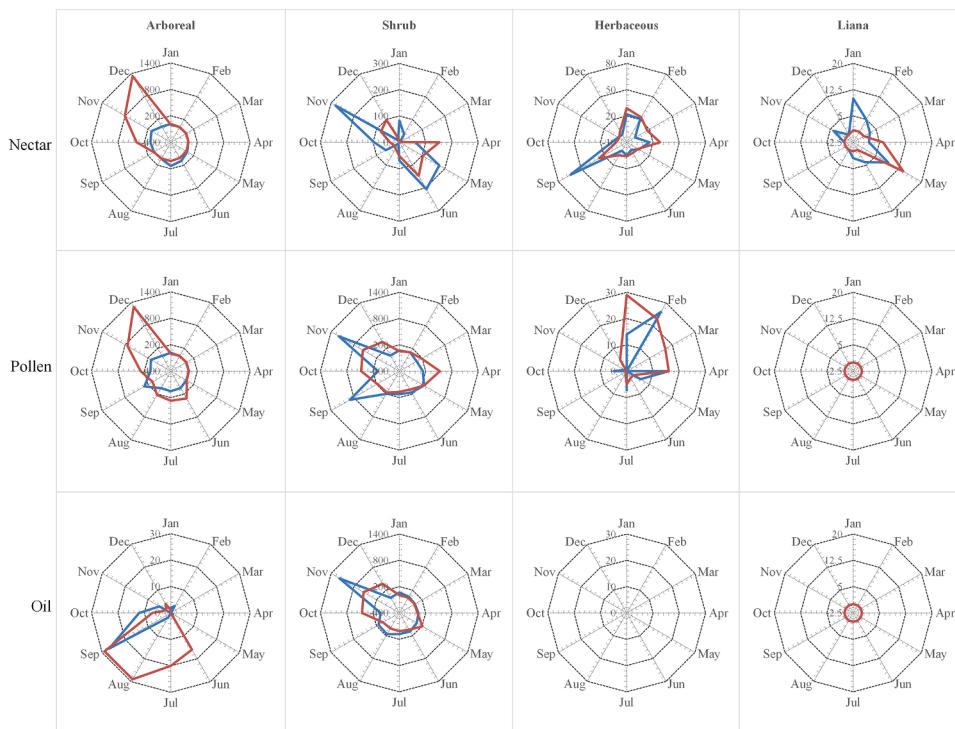


Fig. 5. Circular diagrams of the distribution of floral resources used by pollinators in the vertical strata in cerrado *stricto sensu*, represented by the number of blooming individuals in the Area 3 throughout the two years of survey. The lines show the total of blooming individuals in each month - blue lines represent the year of 2006 and red lines the year of 2007. The months of the year are represented in 360°, in a way that each month period is comprised in a 30° interval - starting from 0° to 30° in January and ending in 360° in December. Concentric circles represent the scale marks of the circular axis.

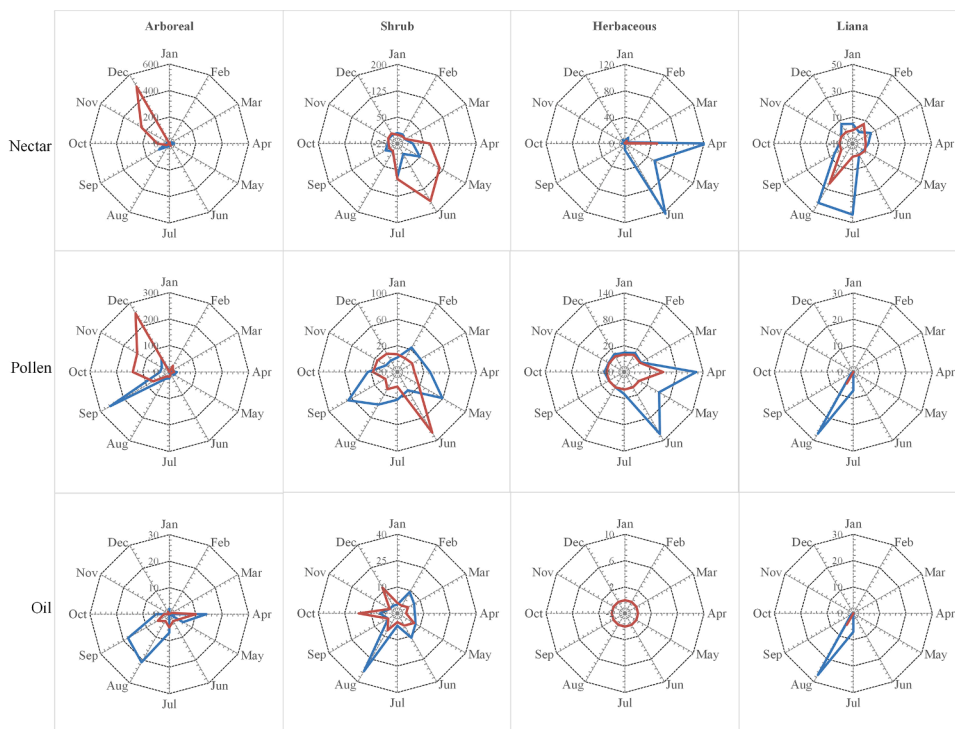


Fig. 6. Circular diagrams of the distribution of floral resources used by pollinators in the vertical strata in cerrado *stricto sensu*, represented by the number of blooming individuals in the Area 4 throughout the two years of survey. The lines show the total of blooming individuals in each month - blue lines represent the year of 2006 and red lines the year of 2007. The months of the year are represented in 360°, in a way that each month period is comprised in a 30° interval - starting from 0° to 30° in January and ending in 360° in December. Concentric circles represent the scale marks of the circular axis.

providing nectar and pollen. In the same stratum, *Byrsonima pachyphylla* Nied was an important provider of pollen and floral oil. In the shrubby stratum, *B. intermedia* was responsible for the peak of pollen and floral oil providers. *Camptosema ellipticum* (Desv.) Burkart (Fabaceae), *Hortia brasiliensis* (Vand.) (Rutaceae), *Palicourea rigida* Kunth. (Rubiaceae) provided nectar and pollen in this stratum, while *T. attenuata* and *Jacaranda decurrens* (Cham.) (Bignoniaceae) provided nectar plus pollen, respectively. These species were also the most representative in the herbaceous

stratum in Area 3, corresponding to the peak of blooming individuals throughout the years. The liana *Odontadenia lutea* (Vell.) Marckgr. (Apocynaceae) was responsible for the blooming peak on nectar availability (supplementary material, Table 1).

Qualea grandiflora Mart. (Vochysiaceae) and *M. guianensis* were the most representative nectar sources in the arboreal stratum during the blooming peak in Area 4. In this same stratum, *B. pachyphylla* and *Byrsonima verbascifolia* (L.) Rich. provided pollen and floral oil. The peak

Table 2

Descriptive statistics, uniformity analysis of phenology (Rayleigh test of uniformity - Z) applied to the circular distribution of floral resources used by pollinators in the vertical strata, represented by the number of blooming individuals in the Area 1 from January 2006 to December 2007, and comparison of phenological patterns between strata (Chi-Squared (χ^2) test) for the three plant resources. ND = No data.

Strata	2006											
	Nectar				Pollen				Oil			
	Arboreal	Shrub	Herbaceous	Liana	Arboreal	Shrub	Herbaceous	Liana	Arboreal	Shrub	Herbaceous	Liana
Observation (N)	229	368	93	48	526	449	93	11	16	189	0	11
Average angle (a)	309.799°	166.058°	118.426°	190.39°	271.617	271.594	118.426	205.82	317.505	319.305	ND	205.82
Concentration (r)	November	June	April	July	October	October	April	July	November	November	ND	July
Test of Rayleigh (Z)	0.436	0.45	0.873	0.218	0.16	0.153	0.873	0.98	0.529	0.306	ND	0.98
Uniformity (p)	43.628	74.663	70.857	2.274	13.526	10.466	70.857	10.557	4.484	17.717	ND	10.557
Chi-Squared test (χ^2) (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	ND	< 0.001
	339.6043				726.5496				285.3611			
	<0.001				<0.001				<0.001			

Strata	2007											
	Nectar				Pollen				Oil			
	Arboreal	Shrub	Herbaceous	Liana	Arboreal	Shrub	Herbaceous	Liana	Arboreal	Shrub	Herbaceous	Liana
Observation (N)	672	331	81	72	1074	669	77	5	33	371	0	5
Average angle (a)	318.945°	114.575°	30.523°	28.949°	315.772	297.199	32.035	225	303.097	314.634	ND	225
Concentration (r)	November	April	February	January	November	October	February	August	November	November	ND	August
Test of Rayleigh (Z)	0.85	0.514	0.771	0.581	0.6	0.371	0.853	1	0.441	0.446	ND	1
Uniformity (p)	484.961	87.525	48.169	24.278	386.326	92.111	56.05	5	6.403	73.89	ND	5
Chi-Squared test (χ^2) (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.001	0.001	< 0.001	ND	0.001
	826.3183				1697.172				608.7628			
	<0.001				0				<0.001			

of blooming individuals in the shrubby stratum was due to *Hyptis crenata* (Pohl) Benth (Lamiaceae), *Vernonia polyanthes*, *Miconia fallax* A. DC. (Melastomataceae) and *H. byrsonimifolia*, the first two nectar plus pollen providers, the third just pollen, and the last one pollen plus floral oil. In the herbaceous stratum *V. scabra* was the responsible for the peak of blooming individuals providing nectar and pollen. Among the lianas, *S. reticulata* and *H. anoptera* represented the peaks of blooming individuals providing nectar plus pollen and pollen plus floral oil, respectively (supplementary material, Table 1).

4. Discussion

We found that the differences in the ecological parameters related to floristic composition among areas, including the diversity of species at different strata, can explain the variations on flowering patterns and floral resource distribution throughout the year. The seasonal flowering patterns described in the study areas were similar to the surveys in other areas in the Brazilian Cerrado plant formations (Batalha et al., 1997; Batalha and Mantovani, 2000; Batalha and Martins, 2004; Mantovani and Martins, 1988; Lenza and Klink, 2006; Oliveira and Gibbs, 2000; Oliveira 2008), with concentration of flowering species in the end of the dry season and in the beginning of the rainy season.

The variation in the seasonal patterns among areas seems to be more related to floristic composition (Silva et al., 2012) and prevalence of certain species in the vertical stratification than to climatic influences. In area 3, for example, where the shrub stratum was more prevalent both in number of species and in number of flowering individuals throughout the year, the flowering pattern was different from areas with lower diversity of species and with more homogeneous distribution of species in the shrubby and arboreal strata (Silva et al., 2012). The flowering distribution and floral resources availability can also be explained by the

representativity of species and individuals from a specific habit or life form. Therefore, all the vertical stratification must be considered in order to understand the dynamics of the floral resource's distribution in a plant community.

Beyond the fluctuations in the flower composition and the distribution of individuals and species among the studied areas, we found variations in the blooming patterns between the years surveyed. These variations illustrate an asynchrony of phenological patterns, e.g., the seasonality that occurred in some areas in the first year did not occur in the same areas along the second year. This could be explained by pluviannual resource allocation of Cerrado plants, where plants store resources in an year or several years (with allocation in vegetative and root parts) before allocate resources for flowering, fruiting, and seed production (Oliveira, 1998; Rizzini and Rizzini 1983). Another important explanation is the natural climatic variation that occur between dry and rainy years, with changes in precipitation and temperature that directly interfere on reproductive success of these seasonality-adapted plants (Lenza and Klink, 2006; Mantovani and Martins, 1988; Oliveira, 1988; Malheiros, 2016). Therefore, the composition of species distributed in the vertical strata may fluctuate among areas, since shrub, herbaceous and liana species are more affected by temperature and climate than arboreal species (Martins and Batalha, 2007; Tannus et al., 2006).

Although seasonality was observed in the arboreal strata, there were species in bloom throughout the year, corroborating other surveys done in the Cerrado (Batalha et al., 1997; Batalha and Mantovani, 2000; Batalha and Martins, 2004; Mantovani and Martins, 1988; Lenza and Klink, 2006; Oliveira, 1988; Oliveira and Gibbs, 2000). Seasonality does not limit the tree species phenology because plants with deeper root systems are less affected by seasonal water fluctuations (Oliveira, 1998; Oliveira, 2008; Tannus et al., 2006). Accordingly, the interaction

Table 3

Descriptive statistics, uniformity analysis of phenology (Rayleigh test of uniformity - Z) applied to the circular distribution of floral resources used by pollinators in the vertical strata, represented by the number of blooming individuals in the Area 2 from January 2006 to December 2007, and comparison of phenological patterns between strata (Chi-Squared (χ^2) test) for the three plant resources. ND = No data.

Strata	2006											
	Nectar				Pollen				Oil			
	Arboreal	Shrub	Herbaceous	Liana	Arboreal	Shrub	Herbaceous	Liana	Arboreal	Shrub	Herbaceous	Liana
Observation (N)	337	640	69	36	714	2164	73	8	19	40	0	2
Average angle (a)	275.249	64.704	17.944	229.66	250.622	142.707	17.781	202.369	286.371	139.423	ND	225
	October	March	January	August	September	May	January	July	October	May	ND	August
Concentration (r)	0.59	0.461	0.999	0.346	0.329	0.435	1	0.986	0.218	0.24	ND	1
Test of Rayleigh (Z)	117.507	135.951	68.874	4.306	77.059	409.514	72.956	7.774	0.905	2.305	ND	2
Uniformity (p)	< 0.001	< 0.001	< 0.001	0.013	< 0.001	< 0.001	< 0.001	< 0.001	0.41	0.099	ND	0.137
Chi-Squared test (χ^2)	874.4732				4067.813				35.63934			
(p)	<0.001				0				<0.001			

Strata	2007											
	Nectar				Pollen				Oil			
	Arboreal	Shrub	Herbaceous	Liana	Arboreal	Shrub	Herbaceous	Liana	Arboreal	Shrub	Herbaceous	Liana
Observation (N)	424	34	453	28	1006	405	394	7	50	13	1	7
Average angle (a)	321.192	23.189	52.522	214.252	300.561	148.229	64.338	179.282	325.13	163.788	285	179.282
	November	January	February	August	November	May	March	June	November	June	October	June
Concentration (r)	0.836	0.242	0.623	0.387	0.576	0.423	0.71	0.8	0.686	0.361	1	0.8
Test of Rayleigh (Z)	296.394	1.997	176.099	4.202	333.636	72.63	198.417	4.481	23.532	1.691	1	4.481
Uniformity (p)	< 0.001	0.136	< 0.001	0.014	< 0.001	< 0.001	< 0.001	0.006	< 0.001	0.186	0.512	0.006
Chi-Squared test (χ^2)	709.2428				1126.954				44.47887			
(p)	<0.001				<0.001				<0.001			

Table 4

Descriptive statistics, uniformity analysis of phenology (Rayleigh test of uniformity - Z) applied to the circular distribution of floral resources used by pollinators in the vertical strata, represented by the number of blooming individuals in the Area 3 from January 2006 to December 2007, and comparison of phenological patterns between strata (Chi-Squared (χ^2) test) for the three plant resources. ND = No data.

Strata	2006											
	Nectar				Pollen				Oil			
	Arboreal	Shrub	Herbaceous	Liana	Arboreal	Shrub	Herbaceous	Liana	Arboreal	Shrub	Herbaceous	Liana
Observation (N)	525	1084	144	39	651	3291	75	0	53	1881	0	0
Average angle (a)	232.249	225.33	285.588	74.639	259.691	276.706	61.359	ND	270.909	299.455	ND	ND
	August	August	October	March	September	October	March	ND	October	October	ND	ND
Concentration (r)	0.46	0.114	0.219	0.404	0.693	0.46	0.528	ND	0.745	0.611	ND	ND
Test of Rayleigh (Z)	110.955	14.135	6.93	6.354	312.253	697.138	20.907	ND	29.394	702.839	ND	ND
Uniformity (p)	< 0.001	< 0.001	< 0.001	0.001	< 0.001	< 0.001	< 0.001	ND	< 0.001	< 0.001	ND	ND
Chi-Squared test (χ^2)	1495.808				7195.454				1727.81			
(p)	0				0				0			

Strata	2007											
	Nectar				Pollen				Oil			
	Arboreal	Shrub	Herbaceous	Liana	Arboreal	Shrub	Herbaceous	Liana	Arboreal	Shrub	Herbaceous	Liana
Observation (N)	2635	734	152	23	3230	3020	102	0	108	1694	0	0
Average angle (a)	324.773	150.244	59.353	118.374	309.292	325.598	54.914	ND	226.91	309.674	ND	ND
	November	June	February	April	November	November	February	ND	August	November	ND	ND
Concentration (r)	0.891	0.249	0.286	0.881	0.534	0.172	0.67	ND	0.75	0.603	ND	ND
Test of Rayleigh (Z)	2090.896	45.352	12.426	17.854	919.54	89.656	45.724	ND	60.804	615.077	ND	ND
Uniformity (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	ND	< 0.001	< 0.001	ND	ND
Chi-Squared test (χ^2)	4927.348				5967.713				1395.891			
(p)	0				0				<0.001			

Table 5

Descriptive statistics, uniformity analysis of phenology (Rayleigh test of uniformity - Z) applied to the circular distribution of floral resources used by pollinators in the vertical strata, represented by the number of blooming individuals in the Area 4 from January 2006 to December 2007, and comparison of phenological patterns between strata (Chi-Squared (χ^2) test) for the three plant resources. ND = No data.

Strata	2006											
	Nectar				Pollen				Oil			
	Arboreal	Shrub	Herbaceous	Liana	Arboreal	Shrub	Herbaceous	Liana	Arboreal	Shrub	Herbaceous	Liana
Observation (N)	286	181	339	112	519	296	339	35	73	79	0	35
Average angle (a)	243.552	168.039	132.961	212.985	263.224	185.877	132.961	219.947	213.674	188.335	ND	219.947
Concentration (r)	0.3	0.613	0.777	0.658	0.566	0.329	0.777	0.984	0.515	0.429	ND	0.984
Test of Rayleigh (Z)	25.694	67.964	204.888	48.511	166.527	32.012	204.888	33.914	19.335	14.567	ND	33.914
Uniformity (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	ND	< 0.001
Chi-Squared test (χ^2)	136.5621				402.6669				18.26738			
(p)	<0.001				<0.001				<0.001			
Strata	2007											
	Nectar				Pollen				Oil			
	Arboreal	Shrub	Herbaceous	Liana	Arboreal	Shrub	Herbaceous	Liana	Arboreal	Shrub	Herbaceous	Liana
Observation (N)	899	437	57	34	718	183	57	5	34	48	0	5
Average angle (a)	328.918	152.851	98.298	219.997	316.058	170.16	98.298	225	165.636	288.408	ND	225
Concentration (r)	0.85	0.829	0.942	0.512	0.659	0.382	0.942	1	0.455	0.389	ND	1
Test of Rayleigh (Z)	650.236	300.473	50.603	8.902	166.527	312.173	32.012	26.76	7.04	7.272	ND	5
Uniformity (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	ND	0.001
Chi-Squared test (χ^2)	1386.104				1331.027				33.17241			
(p)	<0.001				<0.001				<0.001			

between the pollinator activity, the phylogenetic restrictions, and the various strategies of resources allocation (Oliveira, 1998) can explain the flowering patterns better than the climatic patterns. Therefore, rain and climatic patterns may even act as triggers, signaling and synchronizing the occurrence of flowering in some arboreal species, but the flowering period itself may vary from species to species (Oliveira, 2008). On the other hand, the seasonality influences more directly the flowering of the herbaceous strata, many species of which present short life cycles and shallow root systems, depending on water availability of Cerrado soil (Assis et al., 2011; Durigan et al., 2012; Oliveira et al., 2017; Tannus et al., 2006).

The even flowering distribution on the shrubby stratum reveals its contribution to the availability of floral resources in the cerrado *stricto sensu* through the whole year. The asynchrony noted among the flowering stages of the plant species, especially among the different strata, is important to the dynamics and structure of plant communities (Batalha and Mantovani, 2000; Munhoz and Felfili, 2005; Tannus et al., 2006). Flowering asynchrony can be an important strategy to avoid the inter-specific competition of pollinators, being able to maintain pollinators throughout the year (Oliveira and Gibbs, 2002) and it can be a common strategy in the Cerrado. Additionally, plants have other strategies to avoid competition and select their pollinators, such as varying floral morphology, different flowering schedules, and sequential hermaphroditism (Bawa, 1990; Bawa et al., 1985; Bosch et al., 1997; Endress, 1994; Faegri and Pijl, 1979; Oliveira and Gibbs, 1994; Oliveira and Gibbs, 2000; Solís-Montero and Vallejo-Marín, 2017). The flowering synchrony can also be an advantage to the population in terms of conservation, as plant species that bloom simultaneously increase pollinators attraction and promote intraspecific pollen flow (Lenza and Klink, 2006; Moeller, 2004; Primack, 1980).

Our survey showed that in cerrado *stricto sensu* the shrub, herbaceous and liana species are key in the availability of floral resources and maintenance of bee population throughout time, not only during the

cooler and dry season (which was expected to have lower availability of resources), but also at the beginning of the warm and rainy season (when the arboreal species bloom), corroborating other surveys conducted in this plant formation (Andena et al., 2005; Carvalho and Bego, 1997). Although the variations between the distribution of flowering species in the vertical strata and their possible relation to pollinators in Cerrado have been previously mentioned (Martins and Batalha, 2007), the vertical stratification is more commonly described for tropical forests, where it is known to increase the diversity of floral resources to pollinators (Kress and Beach, 1994; Ramalho, 2004). In the Cerrado, in contrast, the physiognomic differences between plant formations lead to horizontal mosaics of floral resources (Oliveira and Gibbs, 2000, 2002), and most studies have focused on the woody species (e.g., Francisco et al., 2016; Lemos et al., 2014; Lima et al., 2015). Our survey showed that this mosaic is also vertical in the cerrado *stricto sensu*.

Regarding all the strata (arboreal, shrubby, herbaceous and lianas), the seasonality was much more discrete than the described in the previous surveys, which highlights the contribution of these strata to the availability of floral resources throughout the year. The distribution of plant species in the different strata in the Cerrado that offer floral resources to pollinators throughout the seasons has been already recognized (Martins and Batalha, 2007). The flowering asynchrony ensures a more or less continuous distribution of floral resources, fundamental to the maintenance of bee diversity in the Cerrado, as they can be found through the whole year foraging among plant formations and vegetation strata (Anacleto and Marchini, 2005; Andena et al., 2005; Carvalho and Bego, 1996; Santos et al., 2004).

5. Conclusion

The vertical and seasonal distribution of floral resources throughout the studied years reinforces the importance of the cerrado *stricto sensu* as a source of floral resources to the bees. The continuous offer in these

areas is possibly even more important when there is less floral resources available in neighboring plant formations. We showed here that this complementarity in availability of floral resources to pollinators occurs not only between plant formations, but also, due to the vertical stratification, within each cerrado *stricto sensu* area. Therefore, as the Cerrado has lost much of its natural areas due to its conversion into extensive plantations and cattle ranching, and as these plants are commonly removed for anthropic activities, their high vulnerability is a conservation concern. Since the cerrado *stricto sensu* is capable of maintaining bee diversity as a result of continuous availability of floral resources throughout the year, each remaining savanna area is important in itself for Cerrado community conservation as a whole. Considering the importance of bees in the maintenance of natural ecosystems and agroecosystems, we emphasize the urge to reduce Cerrado deforestation and to establish conservation policies in order to ensure food supply to pollinators and maintenance of the biodiversity in the region.

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Compliance with ethical standards

The authors declare that there is no conflict of interest. This article does not contain any studies performed on humans or animals by any of the authors.

Credit Author Statement

C.I.S. conceived of the presented idea; conceived and planned the experiments; carried out the experiments.

C.I.S. and A.J.S.P.F performed the calculations and statistical analysis.

C.I.S. and P.E.O. were involved in planning and supervised the work.

All authors discussed the results and contributed to the final manuscript.

All authors contributed to the data analysis and interpretation of the results.

All authors contributed to the writing of the manuscript.

Declaration of Competing Interest

The work is all original research carried out by the authors, and all authors agree with the contents of the manuscript and approved the manuscript and this submission.

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Supplementary materials

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