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**Complementarity between herbaceous and woody plants in providing resources for bees
in a semi-arid tropical climate: insights for conservation**

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*Few phenology studies look at all species with different life and growth forms. We
demonstrate why this approach is a more effective way to evaluate resources for bees and
inform conservation actions.*

Authors' contributions: FJC and FSA conceived and designed the study. FJC performed
fieldwork and conducted data analyses. FJC wrote the manuscript with help of CMAF and
inputs from BMF and FSA. All authors revised the manuscript.

Abstract

The distribution of floral resources in time and space varies according to vegetation strata and to the influence of precipitation and photoperiod on flowering patterns. There are scarce studies jointly investigating the spatio-temporal distribution of plant resources for bees and at the community level, which are critical for planning strategies for their conservation. Here we investigated how herbaceous and woody strata integrate to provide resources (e.g. nectar, pollen, oil) for bees inhabiting fragments of Caatinga dryforest in the northeastern Brazil. We assessed herbaceous and woody strata species composition, abundance and their floral phenodynamics for 18 months in three 0.5-ha plots. We registered bee's plant visits and collected data on abiotic factors to examine how they correlate to flowering patterns. Bees visited approximately 80% of the plant community, composed by a variety of growth (e.g. trees, shrubs, lianas) and life (e.g. phanerophytes, chamaephytes, hemicryptophytes, and therophytes) forms. Water availability was the main variable correlated to arboreal and herbaceous flowering, but photoperiod also played a role in annual and interannual flowering patterns. Both woody (52%) and herbaceous components (48%) similarly contributed to nectar and pollen supplies, while trees were also a source of resin. Herbaceous life forms flowered sequentially during the rainy season, keeping continuous supply until the beginning of the dry season. While growth forms in the woody stratum provided resources relatively constantly throughout the year. The phenological complementarity between different life and growth forms should be considered in bee conservation strategies, aiming to optimize resource availability throughout the year.

Keywords: Caatinga, floral resources, growth forms, life forms, phenology.

Introduction

Bees have an estimated diversity of 20,000 species and are one of the main biotic pollination agents on a global scale. Their importance as pollinators is linked to their strong dependence on floral resources, mainly pollen and nectar (Michener 2007). Bee pollination service benefits approximately 75% of flowering plants and 80% of crops (Klein et al. 2007; Ollerton et al. 2011). Despite their ecological and economic importance, bees have been severely threatened by human activities, i.e., land-use change, agricultural intensification, and use of pesticides. These activities mainly cause the loss of floral resources leading to the decline of bee populations (Potts et al. 2010; Goulson et al. 2015). Furthermore, changes associated with the Anthropocene climate crises (i.e., temperature rises and increases in the frequency of extreme events, such as droughts; IPCC 2014), are likely to decrease the quality and quantity of floral supplies or promote their total loss, posing an even more significant threat to bee populations (Wagner 2020). Therefore, the safeguarding of floral resources is crucial for bees' survival, and their continuum availability throughout seasons is one of the main factors regulating bee populations and diversity (Roulston and Goodell 2011).

How floral resources influence bee populations depends on plant diversity and stratification, and flowering phenodynamics (i.e., flowering duration, total floral abundance, species richness, turnover, scarcity, and resource pulses; Ogilvie and Forrest 2017). Plant diversity and vertical stratification offers a range of resources available at different heights within the plant community. Resources may then be collected, simultaneously or complementarily, at different times of the day or seasonal periods, by a variety of pollinator groups, contributing to the coexistence of species (Aguiar et al. 2013; Venjakob et al. 2016). In turn, climatic factors, such as, rainfall, temperature, and photoperiod, control triggering and duration of

flowering phenodynamics (Forrest and Miller-Rushing 2010), also imposing restrictions on bee foraging (Ogilvie et al. 2017; Lawson and Rands 2019).

The importance of plant communities for bees goes beyond floral resources such as pollen, and nectar. It also includes the supply of nesting resources (i.e. extrafloral resin) and other floral and extra floral resources. For example, bees of the Centridini and Tapinotaspidini tribes collect oils produced in floral glands (elaiophores) to feed their offspring, in replacement to nectar (Michener 2007). Different bee groups use extrafloral resins in nest construction as a protective barrier against microorganisms. These resins tend to be continuously available throughout the year in the plant community (Roubik 1989). Thus, understanding the availability of nesting resources, floral and non-floral food resources is necessary to maintain healthy bee populations (food supply and protective substances) and their species diversity (Requier and Leonhard 2020).

Considering the role of plant diversity in resource supply and the influence of annual climate variation on flowering patterns and, consequently, on the availability of floral resources, studies on floral phenodynamics provide key knowledge for bee conservation, particularly in the face of anthropogenic changes (Morellato et al. 2016). However, such studies should consider an analysis of plant community and its floral phenodynamics that includes life and growth forms (see Monasterio and Sarmiento 1976, Cortés-Flores et al. 2017, Nagahama and Yahara 2019). Life form synthesizes the morphological characteristics linked to the way plants obtain resources to survive in the unfavorable season (Raunkiaer 1934) and growth form describes the community structure (Whittaker 1975). Therefore, the inclusion of those plant attributes to describe phenological patterns allows a better understanding of the influence of abiotic factors on flowering patterns and consequently the distribution of

resources available to pollinators within the community. Also, it is important to consider all species and their respective relative abundances in the community to fully understand the availability of the floral resources. Such community-level analysis enables to quantify how much each plant species contributes resources locally and spatially, thus benefiting bee's populations.

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Phenological studies taking a community approach, as described above, and with a perspective of resource availability particularly for pollinators have not been fully explored in the literature (see Pereira et al. 1989, Rodarte et al. 2008, Quirino and Machado 2014, Aleixo et al. 2014). This information is necessary not only to infer about possible responses of bee populations to ever-changing environments but also to create and implement strategies for the sustainable use of vegetation that ensure the conservation of bee communities and, consequently, the maintenance of pollination as an ecosystem service (IPBES 2016). Most conservation actions implemented so far world widely have been focused on one vegetation component, herbaceous or woody, without considering the phenological complementarity between these components in providing resources for bees (see Garrat et al. 2017, Donkerseley 2019, Timberlake et al. 2019, Requier and Leonhard 2020). Phenological complementarity is fundamental in bee conservation strategies, in particular, to reduce the effects of the temporal deficit of floral resources (Timberlake et al. 2019).

In the northeast Brazilian semi-arid region, floral and non-floral resources have been mainly diminished by deforestation, and they are likely to become more reduced by the Anthropocene climate crisis in the coming decades (Silva et al. 2019). The predicted temperature rises and increase in the frequency of drought events will probably lead to an impoverishment of the local vegetation, an increase of land vulnerability and a growth of

desertification areas (Marengo and Bernasconi 2015). As a consequence, less structurally complex and diverse environments are expected, and there will be a reduction in the number of plant species with different growth habits and specialized pollination systems, directly affecting resource supplies for bees (Silva et al. 2019)

Given the knowledge gap on resources availability for bees from the whole plant community and the vulnerability of Brazilian semi-arid vegetation to land use and climate crisis, we analyzed the availability of floral and non-floral supplies for bees at the community level in three fragments of Caatinga, northeast Brazil. The Caatinga is a seasonally dry forest located in the Brazilian semi-arid region, classified as Tropical Savanna *sensu* Gardner et al. (2020). It is a good study model because it harbors different vegetation growth (trees, shrub, herbs, and lianas) and life (phanerophytes, chamaephytes, hemicryptophytes, cryptophytes, and therophytes) forms (Costa et al. 2007, Quirino and Machado 2014). Also, because insect pollination occurs for 70% of Caatinga plant species, being bees the main pollinator group (Machado and Lopes 2004). Finally, Caatinga climate has high temperatures and frequent drought periods, which replicates the predictions of climate change, offering an opportunity to discuss potential effects of the anthropogenic climate crisis on the supply of resources for bees.

The main questions addressed in the present study were: i) what are the proportions of the plant community and the different vegetation components (herbaceous and woody strata) that provide resources to bees, and what types of resources? ii) how are the annual flowering dynamics in the woody and herbaceous components considering the different life and growth forms, and how does this reflect in the availability of floral resources for bees? iii) how does

the resource availability in each stratum respond to the intra-annual variation in water availability (rainfall and soil moisture)?

Material and methods

Study area

The study area is located in the northeastern Brazil semi-arid region (Fig. S1A), known as the Caatinga Domain (Andrade-Lima 1981) or the Drought Polygon (*Polígono das secas*). The Caatinga Domain has approximately 1,128,697 km² (Brasil MI 2018). Its altitudes vary between 20 and 500 m a.s.l. (Moro et al. 2016). The total average annual rainfall ranges from 400 to 800 mm (Souza et al. 1992), which is usually concentrated in 3-5 months. The annual pattern is erratic with drought years occurring every 3-4 decades and lasting 3-5 years (Sampaio 1995). According to the Köppen system, the semi-arid climate (BSh) predominates in the Caatinga, with summer and autumn rains and dry winter (Alvares et al. 2014). The climate zone corresponding to that classification in the Gardner et al. (2020) system is Tropical Savanna.

The present study was carried out at the Vale do Curu Experimental Farm of the Federal University of Ceará, located in the municipality of Pentecoste, state of Ceará (Latitude: 3°48' South, Longitude: 39°20' West and 80 m a.s.l.) (Fig. S1B). The farm occupies 823 ha, including irrigated crop zones and native vegetation fragments at different stages of secondary regeneration (15-50 years). Based on data from the meteorological station located in the farm (Fig. S1B), the rainfall is concentrated in the first half of the year, usually between January and May, and presents a historical annual average of 759 mm (1970-2019) (Fig. S2A). During

the rest of the year, there is water deficiency in the area that can last from 7 to 11 months. The temperature is high, with an annual average of 28.3 °C (Fig. S2A), which results in high potential evapotranspiration (on average, 1,500 mm per year).

The Caatinga vegetation shows a woody stratum mostly composed of deciduous tree species, many of them bearing thorns. The treetops do not form a real canopy, whose average opening is 18% in the rainy season and 89% in the dry season when the trees lose almost all their leaves (Fig. S3). This canopy opening facilitates the growth of an herbaceous layer composed mainly of annual plants (therophytes), whose richness can be two to three times higher than that of the woody component (see Costa et al. 2007). Succulent plants, especially Cactaceae, are common in both herbaceous and woody strata. As the study area is located near the Curu River, it also has floristic elements of riparian vegetation (see Moro et al. 2015).

Data collection

We selected three Caatinga fragments with more than 30 years of natural secondary regeneration and installed a 0.5 ha plot (50x100 m) in each, considering 2-km equidistance between them (Fig. S1B). This distance between plots was required to ensure independence when sampling bee data, as 1-2 km radius is the foraging area for most bee species (Greenleaf et al. 2007). We collected data on floral phenodynamics for 18 months (August 2017-February 2019) in these three established plots.

We divided the three plots into 50 10x10 m subplots to identify the floristic composition and the abundance of each species per plot, analyze the floral phenodynamics, and determine floral resources availability for bees. We monthly assessed flowering activity of both woody

and herbaceous components in each 50 subplots. To record woody flowering activity, we marked all woody individuals, which presented stem perimeter equal to or greater than 9 cm at the ground level, using metal tags and monthly assessed their flowering phenological state. This was done for all individuals of each species. We assessed flowering intensity of each woody plant (e.g. trees, shrubs and lianas) observed with flowers, using the semi-quantitative method of Fournier (1974). This method visually estimates the percentage of branches covered with flowers, classifying it in one of the five cover classes (0 to 4 range): 0 = absence of phenophase, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, and 4 = 76-100%.

We assessed flowering in herbaceous strata with the semi-quantitative method of Daubenmire (1959), which also uses cover classes to estimate the population abundance of each species. Each month, we estimated the floral cover of herbaceous plants in 25 of the 50 10x10m subplots of each fragment (Fig.S1C). The selection of the 25 subplots for sampling the herbaceous component was random, using the Excel random function. To facilitate visual assessment of the cover, we used four 50x50 cm PVC square within each of the 25 subplots, totaling 100 50x50 cm squares in each fragment (Fig. S1C). In each 50x50 cm square, we estimated the percentage of herbaceous cover and, based on this percentage, the percentage of individuals bearing flowers for each species. We used six classes to estimate floral cover per species: 1 = up to 5%, 2 = 6-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-95%, 6 = 96-100%.

Specialists identified plant taxonomic using exsiccates from samples of branches in the reproductive state (flower buds, flowers, or fruits), which were compared to specimens in the EAC Herbarium (Prisco Bezerra) of the Federal University of Ceará. The names of families, genera, and species were confirmed on the Flora do Brasil 2020 website

(<http://floradobrasil.jbrj.gov.br>). We collected three specimens and deposited them at the EAC Herbarium for each species recorded with flowers in the plots.

Monthly, for one hour during two consecutive days in each plot (between 8:00 and 10:00), we observed the behavior of bees in flowers to determine whether a plant species was used as a supply source. Based on these observations, we determined whether bees collected nectar, pollen, oils, or resins from flowers. We also recorded whether bees collected resins or nectar from other parts of plants, such as the stem or extrafloral nectaries. Thus, we registered, for each plant species the provision of one or more of the following resources: nectar, pollen, oil, extrafloral nectar, floral resin, and extrafloral resin. When it was not possible to visualize a certain bee performing any type of foraging activity in a specific plant, we used information for that plant species available in the literature.

We also classified each plant species according to its growth and life forms and analyzed their phenodynamics. The classification by growth forms followed Whittaker (1975): trees, shrubs, lianas (woody vines), herbs, vines (herbaceous), and epiphytes. The classification of species into life forms followed Raunkiaer (1934), based on the level of protection of the buds and the reduction in the aerial part during the less favorable (dry) season: therophytes, cryptophytes, hemicryptophytes, chamaephytes, and phanerophytes. Lianas and arborescent cacti were considered phanerophytes, and, for the classification of vines, we followed the level of reduction of the aerial part during the dry season (see Raunkiaer 1934).

We collected data on rainfall (mm/month), photoperiod (h/day), and water availability in the soil (% soil moisture/month) to examine the correlation between abiotic factors and floral phenodynamics. This data allows us to discuss potential impacts of foreseen climate warming

and drying on floral phenodynamics and bees' resource supply. Rainfall data were obtained from the meteorological station installed on the farm (Fig. 1A, Fig. S1B). The rainfall distribution pattern from September 2017 to February 2019 followed the historical record for the past 50 years (Fig. 1A, Fig. S2A). Although the annual rainfall for 2018 and 2019 felled above the historical average, until 2017 the area faced a long drought period that lasted almost six years (below the historical average) (Fig. S2B). The photoperiod data were obtained from the Brazilian Interactive Yearbook of the National Observatory (<http://staff.on.br/jlkm/ephemeris/index.php>). The maximum photoperiod was 12.20 h/day in December, and the minimum, 11.54 h/day in June (**Fig. 1B**).

We estimated the percentage of soil moisture based on the difference between the wet and dry weight (gravimetric method) of ten samples per plot per month. We selected ten of the 50 subplots to collect soil samples, spatially distributed to cover the plot area of 50x100 m (Fig. S1D). For this purpose, we divided the plot into three sections (30x50m, 40x50m, 30x50m), selecting three subplots in the first section, four in the second, and three in the third (Fig. S1D). Monthly, we selected different subplots per section and within each subplot we collected approximately 80 g of soil at 15-20 cm depth. In total 540 soil samples were collected and weighed on an analytical balance to three decimal places. We placed the samples in an oven at 100 °C for 72 hours to dry and then weighed them again. The water availability in the soil peaked in March 2018, with a delay of one month in relation to the beginning of rainy season, but as rainfalls increased, the response occurred in the same month (Fig. 1C-D).

Data analysis

We calculated the proportion of plant species visited by bees based on the total plant species bearing flowers recorded in each plot. To characterize this proportion, we calculated the proportion of species by stratum (woody, herbaceous), growth forms, life forms, and resource type. The characterization considered the total number of species visited by bees and the resource used (nectar and pollen). We used species activity and flowering intensity as metrics to describe the phenodynamics of floral resources. The species activity represents the proportion of the woody or herbaceous community in bloom per month in relation to the total of species visited by bees in the plot. Flowering intensity is a measure of floral abundance based on estimated floral cover data for both woody and herbaceous species. We calculated these metrics separately for each plot and by growth and life forms, considering the total of species visited by bees and the type of floral resource used (nectar and pollen).

To calculate the flowering intensity per month of the woody stratum, we divided the sum of all intensity values of the Fournier scale obtained for all individuals of each species by the maximum possible sum attributed to the woody component in each plot (i.e., the total number of individuals in the plot multiplied by four, the highest cover category on the Fournier scale). The flowering intensity of the herbaceous component represents the floral cover estimated monthly using the method of Daubenmire (1959). To estimate the floral cover of herbaceous plants, we calculated, monthly, the frequency per cover class (number of squares with the presence of flowering herbaceous plants per cover class: 1, 2, 3, 4, 5, and 6). Next, we multiplied this frequency by the class midpoint (1 = 2.5, 2 = 15, 3 = 37.5, 4 = 62.5, 5 = 85, and 6 = 97.5) and added together all products of these multiplications to calculate an absolute floral cover value. To express this value in relative terms (%), we divided the absolute cover value by the total number of squares sampled (100 each month).

299 We built phenograms showing species activity and flowering intensity for both woody and
300 herbaceous components to graphically characterize flowering dynamics and, consequently,
301 the availability of floral resources for bees throughout the sampling period. For better
302 visualization of temporal variations in species activity and flowering intensity, the
303 phenograms were constructed based on kernel-smoothed estimates (bandwidth = 3), using the
304 *ksmooth* function of the stats package (R Core Team 2019).

305

306 We performed pairwise cross-correlations between rainfall, photoperiod, and soil moisture
307 (abiotic factors) and community phenodynamics variables (species activity and flowering
308 intensity), classified in life and growth forms, to understand the relationship influence of these
309 abiotic factors (potentially explanatory variables) on flowering phenodynamics (target
310 variables) and its implications on the availability of floral resources for bees. Cross-
311 correlation compares two temporal data series considering temporal lags in that relationship
312 (Legendre and Legendre 2012). Thus, it is possible to identify whether changes in
313 phenological events occur after changes in abiotic factors, lag time (lag), and the correlation
314 between these changes (correlation coefficient). Before estimating cross-correlations, we
315 removed any trend in the data because it needs to be stationary, that is, that the mean,
316 variance, and other statistical properties of the distribution are constant throughout the series
317 (Legendre and Legendre 2012).

318

319 We then built correlograms (cross-correlation graphs) to visualize pairwise cross-correlations.
320 In the graph, the negative lag indicates that the phenological event occurred after the change
321 in the abiotic factor, and the positive lag indicates that the phenological event preceded the
322 abiotic factor. The cross-correlation coefficient at zero lag has the same value as Pearson's
323 linear correlation coefficient, showing that the series occur simultaneously, with no lag

between the data. Therefore, it indicates a response in the same month of the change in the abiotic factor. We used the *ccf* function (stats package) to calculate correlations and built correlograms and, the *detrend* function (pracma package, Borchers 2019) to remove the trend in the data. All functions were performed on the R platform (R Core Team 2019).

Results

Floristic composition and diversity of floral resources

In total, we analyzed the floral phenodynamics of 4402 individual woody plants, belonging to 38 morphospecies, 34 genera, and 18 families, recorded in the three 0.5 ha sampling plots. The families with the largest number of species were Fabaceae (10 spp.), Euphorbiaceae (6 spp.), and Bignoniaceae (3 spp.). The number of individuals and species by plot were: plot 1 (1634 ind, 31 spp.), plot 2 (1180 ind, 25 spp.), and plot 3 (1588 ind, 25 spp.). The woody species with the highest relative density per plot were *Sebastiania macrocarpa* (18%), *Croton blanchetianus* (17%), *Combretum leprosum* (10%), *Cenostigma bracteosum* (9%), *Mimosa caesalpiniiifolia* (6%), *Cordia oncocalyx* (5%), *Piptadenia stipulacea* (4%), *Amburana cearensis* (4%), *Bauhinia cheilantha* (4%), and *Fridericia* sp (Table S1).

For the herbaceous component, we recorded 44 morphospecies, grouped into 32 genera and 16 families in the three 0.5 ha sampling plots. The most speciose families were Asteraceae (8 spp.), Fabaceae (5 spp.), Acanthaceae, Commelinaceae, and Convolvulaceae (4 spp. each). The morphospecies with the highest cover percentage were *Ruellia paniculata* (15%), *Commelina erecta* (7%), *Dicliptera mucronifolia* (6%), *Justicia* aff. *thunbergioides* (5%),

Ipomoea sp.3 (4%), *Desmodium* sp. (3%), *Alternanthera brasiliana* (3%), *Spermacoce* sp. 2 (3%), *Oxalis divaricata* (3%), and *Mesosphaerum suaveolens* (2%) (Table S1).

The total flora analyzed in the three plots included 82 species (44 herbaceous and 38 woody). Of these, 69 were visited by bees: 40 (90%) herbaceous morphospecies and 29 (76%) woody species, representing 84% of the total species found in the community. However, in the individual analysis by plot, the woody and herbaceous strata showed similar relative importance in the proportion of species/morphospecies visited by bees (Fig. 2, Fig. S4).

Although we recorded bees visiting all types of growth forms (trees, shrubs, lianas, herbs, and vines), they mostly visited trees (38%) and herbs (41%) (Fig. 2, Fig. S4). The classification by life forms showed that bees visited phanerophytes, chamaephytes, hemicryptophytes, and therophytes, but phanerophytes (52%) and therophytes (26%) were the two life forms with the highest percentage of species visited (Fig.2, Fig. S4). Regarding the type of floral resource, 50% of plant species were visited for both nectar and pollen (classified as nectar-polliniferous), while 42%, were visited for exclusively one of the two (25% nectar, 17% pollen, Fig.S4). The remaining 8% corresponded to a single species visited for oil (*Angelonia* sp., Portulacaceae) and four other species visited for resins only (*S. macrocarpa*) or for resins, nectar, and/or pollen together (*C. bracteosum*, *C. blanchetianus*, *Myracrodruon urundeuva*) (Fig. S4, Table S1).

Nectar and pollen availability were analyzed separately per growth and life forms by stratum. We found similar proportions of species in the two strata (51% woody and 49% herbaceous) providing pollen and a relatively higher proportion of woody species providing nectar (59% woody and 41% herbaceous) for bees (Fig. 2). This difference reflects a great proportion of tree and liana species providing nectar in the woody stratum. We recorded bees visiting lianas

only for nectar (Fig. 2). Among herbaceous plants, the proportion of chamaephytes and therophytes species providing nectar was similar (~ 20%), but the proportion of therophytes providing pollen was higher (29%) than chamaephytes (12%). Hemicryptophytes only provided pollen (Fig. 2). Only the woody component (trees) provided resins, and a therophyte species provided oils (Table S1).

Phenodynamics of floral resources

In general, considering the three plots (landscape level), we recorded a continuous availability of floral resources in 17 out of the 18 months studied. However, species activity and flowering intensity peaks occurred mainly in the transition period (May-July) from the rainy to the dry season in 2018 (Fig. 3, Fig. 4). The woody stratum showed activity in 15 out of the 18 months and the herbaceous stratum in 10 out of the 18 months analyzed. Simultaneous activity of both two strata occurred in periods of four to six months, which defined the peak of floral resources (Fig. 3, Fig. 4). The period of the highest resource availability (more species active and more intense flowering) was shorter for nectar (April to August 2018, Fig. 3, Fig. 4) than the period of pollen availability, which lasted from January to August 2018 (Fig. 3, Fig. 4). Oil was available only in June 2018, with a cover percentage below 1% of the plot (Table S1).

Out of the 29 phanerophyte species visited by bees, only 16 showed flowering activity during the study. However, the activity was well distributed among months (one or two different species bloomed each month per plot) (Fig. 3). Regarding flowering intensity of the woody component, we recorded two peaks, the first in February 2018, at the beginning of the rainy season, exclusively by the flowering of *C. blanchetianus* trees, and the second, between May

and August 2018, at the end of the rainy season and the beginning of the dry season, mainly by the flowering of the *A. cearensis* trees (Fig. 3). Trees were the main resource supply in the rainy season and in the beginning of the dry season, when we recorded higher species flowering activity (Fig. 4). While shrubs and lianas stood out during the last months of the dry season (October-December) and in the transition between the dry and rainy seasons (December-January) (Fig.4). Together, these different growth forms kept flowering supply for bees during all seasons

Herbaceous species flowering activity concentrated in the rainy season (February-May 2018) and in the beginning of the dry season (June –September 2018), with species activity and flowering intensity peaks in May, with up to 15 species flowering simultaneously per plot (55% of species) (Fig. 3, Fig. 4). The analysis by life forms revealed that the first species bearing flowers were hemicryptophytes (maximum activity in February), followed by terophytes (maximum activity in May), and chamaephytes (maximum activity in July), whose flowering extended until September, with *R. paniculata* being the only chamaephyte species active in that month (Fig. 3, Table S1).

Correlation of flowering phenodynamics with abiotic factors

Life and growth forms cross-correlation analysis allowed us to verify the relationship of between abiotic factors and flowering phenodynamics of the herbaceous and woody strata (Fig. 5). We found significant positive correlations in the woody strata between tree's phenodynamics (species activity and flowering intensity) and rainfall and water availability in the soil, with a three to four months lag. The correlation between tree's phenodynamics and photoperiod was significantly negative and showed no time lag, indicating a prompt response

to the decrease in the number of light hours per day. Shrub's activity pattern was the opposite of trees, showing a significant positive correlation with increased photoperiod and negative correlations with decreased rainfall and water availability in the soil. Correlations were positives but not significant for shrub's flowering intensity. Lianas' phenodynamics was positively correlated with rainfall and soil moisture, but started a month in advance (positive lag), indicating a rapid response to the first rains, i.e., those that started before the peak of water availability (maximum rainfall and soil moisture) of the rainy season (Fig. 5). Their correlation with photoperiod was positive but not significant.

In general, herbaceous flowering phenodynamics showed a significant positive correlation with rainfall and soil moisture and a negative correlation with photoperiod, showing a direct response to both the increase of water availability and the decrease in the number of light hours per day (Fig. 5). However, the time lag or advance in relation to abiotic factors differed among life forms. Chamaephytes showed a time lag (three months) in relation to the peak of water availability but not in relation to the decrease in photoperiod (Fig. 5).

Hemicryptophytes did not show a time lag in relation to the peak of water availability but showed a time advance (three months) in relation to the minimum photoperiod (Fig. 5).

Finally, therophytes showed an intermediate pattern between cryptophytes and hemicryptophytes, with two months lag in relation to the peak of water availability and one month in advance before the minimum photoperiod (Fig. 5).

Discussion

Our results showed that approximately 80% of species from both herbaceous and woody strata constitute an important source of floral and non-floral resources for bees at the

landscape level. This bi-stratified community presents intra- and interspecific temporal variation in phenodynamics, which combined, can provide a continuous supply for bees throughout the year, including during the dry season, when almost all plant species lose their leaves.

The importance of herbaceous and woody plants in the provision of pollen and nectar for bees has been previously highlighted (Rodarte et al. 2008, Quirino and Machado 2014, Pereira et al. 1989) for Caatinga vegetation, including for the same location studied here (Pereira et al. 1989). Although these studies had already emphasized the importance of floristic diversity and interspecific phenological differences in the supply of floral resources throughout the year, they missed important components for a complete approach on resources availability. They did not analyze the types of resources (i.e. pollen, nectar, extra floral resources) collected by bees, or their distribution in the vertical vegetation structure, neither how they vary over time, and their analysis was limited to a small number of individual per species, consequently, it was not possible to quantify the contribution of each species to the supply for bees.

Analyses at the community and landscape levels, like our study, show that woody plants with different growth forms (trees, shrubs, lianas) and herbaceous plant with different life forms (phanerophytes, chamaephytes, hemicryptophytes, and therophytes) are complementary in the supply of resources along the year. For example, we show that herbaceous plants supply goes from the beginning of the rainy season until the first months of the dry season (February-August). However, hemicryptophytes, therophytes and chamaephytes herbs are the mainly source at different periods of this season, i.e., at the beginning, middle and final, respectively. Also, woody plants are important during the dry season (October-January), being this supply

mainly provided by shrub and lianas. Additionally, we registered that the extrafloral resin supplies are related to trees with high abundance in the sampled plots (*C. blanchetianus*, *C. bracteosum*, and *S. macrocarpa*), which highlights the need to consider the provision of non-floral resources for bees when analyzing plant communities. Therefore, our study reinforces the importance of phenological complementarity in the design of conservation actions for bee populations as suggested by Timberlake et al (2019). However, our distinguished approach provided a better understanding of the complementarity of different vegetation strata in keeping resource availability for bees throughout seasons. That said, for more effective conservations actions we suggest to carefully consider life and growth forms of plant species for provide both vertical stratification and temporal availability of resources throughout the year.

For the herbaceous strata, it is worth mentioning that vegetation management actions should consider the reconciliation between bee conservation and productive activities like extensive cattle, sheep, and goat farming, that are very common in arid and semiarid regions like our study (Sampaio 1995). This is because extensive livestock farming prevents palatable herbaceous species (mainly therophytes) from completing their life cycle in the rainy season and, consequently, soil seed bank is not restored and the flora is not replenished in the following year (Mamede and Araújo 2008). Thus, such activities threat the resource supply provided by the herbaceous component (50% therophytes life form), including oil-producing species like *Angelonia* sp. (Plantaginaceae). This plant species is one of main oil sources for bees of the genus *Centris*, key pollinators of wild and cultivated plants in the Caatinga (Aguiar et al. 2003).

The cross-correlations analysis between phenological variables and abiotic factors (rainfall, soil moisture, and photoperiod) by life and growth forms allowed a more refined understanding of the relationship between water availability (rainfall and soil moisture), photoperiod and flowering patterns. As expected, we found significant correlations between rainfall and flowering patterns supporting previous studies in seasonally dry vegetation (e.g. Pereira et al. 1989, Machado et al. 1997, Borchert et al. 2004, McLaren and McDonald 2006, Amorim et al. 2009, Lima and Rodal 2010, Cortés-Flores et al. 2020), that found flowering of woody and herbaceous components positively correlating with rainfall, which is the main abiotic factor in short supply in these environments. However, by looking not only at rainfall but also at soil moisture, our analysis augmented previous evaluation, presenting a more general view of how water availability is related to plant's dynamics. Also, by building correlograms, we were able to jointly visualize the monthly variation of the different studied variables and pinpoint their time lags, an interesting data absent from previous studies. For example, water availability (resulted from the first rains at the beginning of the year) was significantly and positively correlated with the activity of lianas. This aligns with the fact that lianas in the Brazilian semi-arid have superficial roots and a highly efficient vascular system that quickly uses the water from the first rains and avoids subsequent competition with trees in the rainy season as demonstrated by Carvalho et al. (2016).

In turn, we found that the photoperiod decrease, observed from end of rainy to beginning of dry season (June to August), was positively correlated with flowering of herbaceous plants (chamaephytes and therophytes) and deciduous trees. Likewise, the photoperiod increase, observed from end of dry to beginning of rainy seasons (September to December), was related to the flowering of evergreen woody trees at the end of the dry season. These results follow similar findings observed in deciduous seasonal forests (Rivera and Borchert 2001, Borchert

et al. 2004, and Cortés-Flores et al. 2020), and in the Caatinga (Lima and Rodal 2010). Also, it has been previously discussed (Rivera and Borchert 2001) that photoperiod control of flowering in tropical climate areas with prolonged and severe dry seasons, as in the Caatinga, represents an adaptive response to optimize reproduction, and it includes the induction of flowering when photoperiod decrease, leading into resource availability also in unfavorable times. Thus, our results also point out to the importance of implementing plant species with different responses to abiotic factors to ensure a continuous supply of resources for bees throughout the year.

The species *A. cearensis*, *Cochlospermum vitifolium*, *Commiphora leptophloeos*, *Cynophalla flexuosa*, *Ziziphus joazeiro*, and *Handroanthus impetiginosus* bear flowers in the dry season. Although they are not very abundant, the fact they bloom in the very dry season when most plants have lost their leaves makes them a treasurable resource and as their flowers stands out in the scarce vegetation, they are favored with a higher frequency of pollinator visits. Thus, they are “not to miss” candidates when planning plant implementations for bee maintenance. For example, *C. vitifolium*, whose flowers need vibration to release pollen, is among the most important pollinating plants for large bees, such as *Xylocopa*, which forage all year in the Caatinga (Roubik et al. 1982). Hence, it is imperative to include such species in a program for reforestation and restoration of degraded areas for bee conservation.

Despite the clear relationship between photoperiod and flowering in dry vegetations, such as in Caatinga, water availability (rainfall and soil moisture) is the determining factor of flowering, i.e., the ultimate cause (Borchert et al. 2004). Species that flower in the dry season also depend on the water stored in the root or stem system during the rainy season to produce flowers. Although expected, some woody species did not flower during our study timeframe.

This was not because they have supra-annual flowering, but because of water shortage, as these species emit flowers annually under satisfactory water conditions. For example, *C. leprosum* and *Libidibia férrea*, showed an annual flowering pattern in phenological studies carried out during several years of regular rainfall as reported by two other Caatinga studies (Machado et al. 1997, Amorim et al. 2009). A long period of below-average rainfall (approximately six years of drought) preceded our study, and, as reported by Pereira et al. (1989), when there is not enough water availability, some species can go years without flowering. In a general context, the most profound implication of this is that the resource supply provided by these species is likely to disappear with global warming. A higher frequency of droughts and increased temperatures are predicted for the Brazilian semi-arid region (Marengo and Bernasconi 2015) as a result of climate change. Thus, *C. leprosum*, *Libidibia férrea* and other species will likely remain longer and longer without flowering, compromising the survival of bee species dependent on their floral supplies.

The analysis of the resource availability in the vertical structure of the bi-stratified plant community (herbaceous and woody) and their temporal distribution in seasonally dry environments demonstrates that in the rainy and dry seasons, both strata are important for bee conservation as they differ in resource supply. In summary, in the planning and implementation of management actions for the reforestation and restoration of degraded areas to mitigate current scenario and future climate change effects associated with bee conservation (less water availability, less flowering, less resources acquisition), it is necessary to consider the floral phenodynamics variation in the vertical vegetation structure and the temporal distribution of flowering to provide the most significant possible supply of resources for feeding (pollen, nectar, and oils) and nest-building (resins).

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Declarations

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Figure Captions

Figure 1. Climatic characterization, photoperiod, and water availability in the soil in a Tropical Savanna (Caatinga) area in northeastern Brazil. A) Walter-Lieth climate diagram comprising the three years of the study (2017-2019). B) Monthly photoperiod. C) Monthly soil moisture in relation to the monthly accumulated rainfall. The blue line represents the mean of the three plots, and the value of each plot represents the mean of ten soil samples. D) Cross-correlation between soil moisture and rainfall confirming the initial lag in soil moisture in relation to rainfall (significant correlations above the dashed line on the negative side of the x-axis) and subsequent maintenance of water availability (significant correlations at zero and on the positive side).

Figure 2. Composition of plant species visited by bees, classified by type of assemblage, growth form, life form, and resource available in a Tropical Savanna (Caatinga) area in northeastern Brazil. The values represent the total mean of the proportion found in the three plots. Figure S4 shows the individual data per plot.

Figure 3. Phenodynamics of the plant community visited by bees and classified by the type of floral resource (nectar and pollen) according to life forms in a Tropical Savanna (Caatinga) area in northeastern Brazil. The left side represents species activity (percentage of species bearing flowers), and the right side, flowering intensity (percentage of the canopy with woody individuals bearing flowers of all flowering species and percentage of soil cover with herbaceous plants bearing flowers). The shaded areas in the background represent monthly accumulated rainfall and soil moisture.

Figure 4. Phenodynamics of the plant community visited by bees and classified by the type of floral resource (nectar and pollen) according to growth forms in a Tropical Savanna (Caatinga) area in northeastern Brazil. The left side represents species activity (percentage of species bearing flowers), and the right side, flowering intensity (percentage of the canopy with woody individuals bearing flowers of all flowering species and percentage of soil cover with herbaceous plants bearing flowers). The shaded areas in the background represent monthly accumulated rainfall and soil moisture.

Figure 5. Cross-correlations between phenodynamics (species activity and flowering intensity) of plants visited by bees and abiotic factors (rainfall, soil moisture, and photoperiod) in a Tropical Savanna (Caatinga) area in northeastern Brazil, according to life and growth forms. Significant correlations (bars above the dashed line) on the negative side of the x-axis indicate the lag in months in variables' responses to the abiotic factor. Significant correlations on the positive side of the x-axis indicate that the phenological event preceded the abiotic factor. Correlation at zero lag indicates a response in the same month of the change in the abiotic factor

Figure 1

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