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Reproductive phenology of cacti species in the Brazilian Chaco

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ABSTRACT

In this study, we made monthly assessments of the reproductive phenology of ten cacti species that are widely distributed in the Brazilian Chaco over a 2-year period. We tested whether different climatic regimes in this region promoted the evolution of different reproductive strategies among cacti species. We applied circular statistics and the Rayleigh test to determine whether flowering and fruiting were seasonal and to detect significant periodic patterns. Multiple linear regressions were used to determine the influence climatic variables had on the number of flowers and fruits produced by each species. The flowering and fruiting periods began during the rainy season and peaked in November and January, respectively. Annual and continuous patterns were observed, which presented extended durations. The timing of flowering and fruiting was positively associated with day length and temperature. Rainfall was not significant in any of the models. In the Brazilian Chaco, the cacti reproductive phenophases were triggered by changes in day length and temperature. The similarity in flowering and fruiting patterns among the cacti species with extended durations generated a significant amount of overlap in flowering and fruiting, which may be a strategy to maintain pollinator and seed disperser populations in this environment.

1. Introduction

Reproductive phenology involves temporal patterns of resource availability for consumers, which in turn strongly influences the reproductive success of plants through pollination, seed dispersal, pre-dispersal seed predation, and herbivory (Williams et al., 1999; Elzinga et al., 2007). Several climatic variables (such as rainfall, temperature, day length, irradiance, and relative humidity) can trigger and regulate reproductive phenophases (Rathcke and Lacey, 1985; Borchert et al., 2005; Pfeifer et al., 2006; Dahlgren et al., 2007; Seghieri et al., 2009; Staggemeier et al., 2010; Munson and Sher, 2015). Biotic interactions, such as pollination and seed dispersal, may also determine the timing, length, and synchrony of flowering and fruiting (Wright, 1996; Elzinga et al., 2007; Staggemeier et al., 2010). Conversely, temporal patterns of flowering and fruiting of some plant species can potentially affect other plants through competition and/or facilitation of pollination and seed dispersal, resulting in community level consequences (Moeller, 2004; Elzinga et al., 2007; Burkle and Alarcon, 2011; Gomes et al., 2017).

Open biomes in eastern South America, including the Caatinga, Cerrado, and Chaco, are diagonally organized and referred to as the Dry

Diagonal (Werneck, 2011, Fig. S1). All of these biomes are seasonally stressed by drought and have unique biotas (Furley and Metcalfe, 2007; Mooney et al., 1995). According to Gentry (1995), seasonally dry tropical forests grow where rainfall is less than 1600 mm/year and less than 100 mm for at least 5–6 months of the year (e.g. Caatinga). Although Chaco forests have a seasonal climate with a dry period for several months, they are not considered seasonally dry tropical forests due to their distinct composition of flora, climate, soils, and topographic conditions (Pennington et al., 2000; Prado, 1993).

In the Chaco, annual rainfall presents an E – W gradient, ranging from 1000 mm/year in its eastern portion to less than 550 mm/year in the western portion. Accordingly, the climate is graded and contains distinct subregions: Humid Chaco, Dry Chaco, and Montane Chaco (TNC et al., 2005). The Brazilian Chaco lies within the humid Chaco portion (Werneck, 2011), and presents higher humidity than other parts, but is still considered a semiarid (Prado, 1993; Werneck, 2011) or arid environment (Bullock, 1995; Carvalho and Sartori, 2014).

In tropical environments with defined seasonality, reproductive phenophases are known to be positively correlated with different abiotic factors. Furthermore, there is a high level of synchrony between

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phenological events and the rainy season (Machado et al., 1997; Williams-Linera and Meave, 2002; Batalha and Martins, 2004; Morellato et al., 2013). For example, in the Brazilian Caatinga, reproductive events are seasonal and concentrated in the rainy season, and flowering and fruiting peaks occur at the beginning and end of the rainy period (Machado et al., 1997; Amorim et al., 2009; Lima and Rodal, 2010; Quirino and Machado, 2014). In contrast, reproductive phenophases of the woody community in the Brazilian Chaco present less seasonality, and no correlations have been observed between flowering and fruiting and the climatic factors studied (Carvalho and Sartori, 2014). These results differ from those typically found in seasonal environments (Carvalho and Sartori, 2014).

Cactaceae are one of the most diverse families in the Neotropics, with 1480 recognized species (Goettsch et al., 2015). This family represents an important floristic element of the Caatinga and Chaco vegetation in Brazil (Pennington et al., 2000). These plants are commonly found under extreme conditions in water-stressed environments (Mutke, 2015). These species have been able to colonize these extreme environments due to a variety of morphological, physiological, and ecological adaptations, as well as their reproductive versatility (Nobel, 2002; Mandujano et al., 2010). For example, species that flower and fruit during the dry season produce seeds at the beginning of the rainy season (Valiente-Banuet et al., 1996; Cuéllar, 2000; Fleming et al., 2001; Pavón and Briones, 2001; Petit, 2001; Bustamante and Búrquez, 2008), a period that favors germination. Therefore, when species bloom in the dry season, climatic factors, such as temperature and day length, likely trigger flowering.

Studies about different cactus species in seasonal formations around the world have demonstrated that the timing and intensity of reproductive phenological patterns are mostly affected by variations in rainfall and/or temperature, with examples from the Sonoran Desert (Bowers, 1996; Bustamante and Búrquez, 2008), Bolivian Chaco (Cuéllar, 2000), Tatacoa desert in Colombia (Ruíz et al., 2000), Curaçao Island in Venezuela (Petit, 2001), Caribbean Dry Forest of Mona Island (Rojas-Sandoval and Meléndez-Ackerman, 2011), and Brazilian Caatinga (Quirino, 2006; Gomes et al., 2014; Gomes et al., 2017). However, the influence of rainfall and temperature on phenology is not uniform for all cacti species and their effects on reproductive timing can be positive, negative, or null (Rojas-Sandoval and Meléndez-Ackerman, 2011). Nevertheless, other climatic factors have been completely ignored in these studies and remain poorly explored (for exceptions see Bowers, 1996; Rojas-Sandoval and Meléndez-Ackerman, 2011).

One untested hypothesis is whether different climatic regimes have promoted the evolution of different reproductive strategies among cacti species (Rojas-Sandoval and Meléndez-Ackerman, 2011). The Brazilian Chaco has a distinct climate compared to other seasonal regions like the Caatinga and Dry Chaco, especially in regard to rainfall volume. This region lies within the humid region of the Chaco, a relatively wetter area with a 4 month dry season. During the rainy summers, maximum temperatures reach 49 °C, and during dry, cool winters there are occasional frosts (Prado, 1993; Pennington et al., 2000). Due to differences in the intensity of seasonality in the Chaco, flowering and fruiting patterns may present distinct phenological responses to climatic factors compared to other seasonal areas with more intense and prolonged dry seasons, such as the Caatinga. Herein, we ask which climatic variables trigger cacti reproductive events in the Chaco environment, which displays distinct seasons.

We monitored the reproductive phenology (flowering and fruiting) of ten native cactus species over a 2-year period to evaluate which strategies these plants use to ensure reproductive success in the Brazilian Chaco. We addressed the following questions: Is there seasonality to the flowering and fruiting of Cactaceae in the Brazilian Chaco? Which climatic variables trigger cacti reproductive events in this environment? Do reproductive phenological patterns differ between the cacti species?

2. Material and methods

2.1. Study site

Fieldwork was conducted from October 2014 to September 2016 in an area of Brazilian Chaco located in the São Fernando Ranch, Porto Murtinho municipality, Mato Grosso do Sul state (21°37'51.0" S and 57°49'29.4" W) (Fig. S1). The Brazilian Chaco is restricted to the extreme western edge of Mato Grosso do Sul and presents floristic similarities with the Chaco *sensu stricto* of Paraguay and Argentina (Prado et al., 1992). The study site consisted of a 99.2 ha Chaco remnant. It is characterized by the presence of a discontinuous shrub layer containing thorny and microphyllous species, as those in Fabaceae, Bromeliaceae and Cactaceae. It is classified as a woody steppic savanna, which is a Chaco vegetation subtype (Sartori, 2012). The site contains native vegetation in a legal reserve area (protected natural areas inside private rural properties - farms), which is protected by the Brazilian Forestry Code, a federal law that establishes bases for the defense of Brazilian natural resources (Brasil, 2012).

The climate in the study area is tropical warm with well-defined rainy and dry seasons (Brasil, 1997), displaying a hot and wet summer and a dry and cool winter with occasional frosts (Pennington et al., 2000). The average (1979–2010) annual temperature and rainfall were 27 °C and 1193 mm, respectively. The climatic data for that period was obtained from CPC - Climate Prediction Center (rainfall) and CFSR - Climate Forecast System Reanalyses (temperature), both available in CEMTEC (<http://www.agraer.ms.gov.br/cemtec>). Rainfall primarily occurs from November to February (rainfall \geq 100 mm) and the dry season occurs from June to September (Fig. S2). March, April, May, and October are transitional months when sparse rainfall reaches up to 100 mm, without water deficits (Freitas et al., 2013).

During the study period (2014–2016), the average annual temperature was 25.4 °C and the day length ranged from 10.50 h to 13.26 h. The annual rainfall varied between the study years and ranged from 1138 mm (January–December 2015) to 858 mm (January–December 2016). Higher monthly rainfall was recorded in November in both years (Fig. S2). The climatic data for the study period was obtained from a local station and is available at CEMTEC (Monitoring Center for Weather, Climate and Water Resources of the State of Mato Grosso do Sul, Brazil - station code: A723; 79 m a.s.l.). The day length for 21° S latitude was calculated using the Online Photoperiod Calculator (Lammi, 1996–2015).

2.2. Data collection and analyses

Phenological monitoring was carried out in 10 plots (200 × 10 m) located 50 m from each other, yielding a total sample area of about 2.0 ha. We carried out monthly phenological monitoring of 138 adult individuals belonging to 10 different cacti species (Table 1; Fig. 1). These were the most representative cacti species in the study area. A recent checklist indicates reasonable diversity of cacti and no endemic species in the Chaco vegetation of Mato Grosso do Sul state (Zappi et al., 2018). Cactaceae is represented by 16 species in the Brazilian Chaco (Brazil Flora Group, 2015), including columnar (8), globose (3), coplanar (2), epiphyte (2) and shrubby (1) species, which are potentially pollinated and dispersed by biotic vectors (Gomes and Araujo, 2015, Table 1). These species are native and locally threatened by the continuous deforestation for cattle ranching, which has already largely affected the Brazilian Chaco (Silva et al., 2008, 2011).

Phenological monitoring was conducted on a monthly basis from October 2014 to September 2016 by counting the numbers of flowers and fruits on each individual plant in the studied plots. The flowers and ripe fruits were counted to estimate resource availability for pollinators and seed dispersers. We calculated the first month of flowering and fruiting, the peak date of these events, and the total number of months that a species was reproductively active. We defined flowering and

Table 1

Cacti species in a Chaco remnant in Porto Murinho, Mato Grosso do Sul, Brazil and respective life-forms (sensu Anderson, 2001), pollination (sensu Faegri and Pijl, 1979) and seed dispersal syndromes (sensu Pijl, 1982). Flowering and fruiting strategies and duration (adapted from Newstrom et al., 1994). Conservation status follows the IUCN Red List. LC = Least concern and VU = Vulnerable. Voucher numbers at CGMS Herbarium, Federal University of Mato Grosso do Sul, Campo Grande, Brazil. N = number of individuals monitored per species.

Species	Life-forms			N	Voucher	Conservation status	Pollination	Seed dispersal	Flowering		Fruiting	
	Columnnar	Shrubby	Globose						Strategy	Duration (N of months)	Strategy	Duration (N of months)
<i>Cereus bicolor</i> Rizzini & A. Mattos	Columnnar	Shrubby	Globose	15	29257	LC	bat	birds/bats	Annual	Extended (7)	Annual	Extended (8)
<i>Cleistocactus baumannii</i> (Lem.) Lem. subsp. <i>baumannii</i>	Shrubby	Shrubby	Shrubby	15	49912	LC	hummingbird	birds	Continuous	Extended (10)	Annual	Extended (8)
<i>Echinopsis rhodotricha</i> K.Schum. subsp. <i>chacoana</i> (Schatz) Braun & Esteves	Columnnar	Shrubby	Shrubby	15	36887	LC	moth, bees	birds, lizards	Annual	Extended (8)	Annual	Extended (9)
<i>Pringlea schilinzkyana</i> (K.Schum.) Britton & Rose subsp. <i>conceptionensis</i> (Buining & G.Moser) Braun & Esteves	Columnnar	Shrubby	Shrubby	12	51935	VU	bees	ants	Annual	Intermediate (4)	Annual	Intermediate (3)
<i>Harrisia balansae</i> (K.Schum.) N.P. Taylor & Zappi	Climbing	Climbing	Climbing	12	41477	LC	moth	birds, bat	Annual	Extended (7)	Annual	Extended (5)
<i>Harrisia tortuosa</i> (J.Forbes ex Otto & A.Dietr.) Britton & Rose	Climbing	Climbing	Climbing	12	35455	LC	moth	birds/bats	Annual	Extended (7)	Annual	Extended (5)
<i>Opuntia elata</i> Salm-Dyck	Shrubby	Shrubby	Shrubby	15	53327	LC	bees	birds	Annual	Extended (7)	Annual	Extended (8)
<i>Opuntia retrorsa</i> Speg.	Shrubby	Shrubby	Shrubby	15	49911	LC	bees	birds	Annual	Extended (7)	Annual	Extended (8)
<i>Procereus saxicola</i> (Morong) N.P. Taylor	Shrubby	Shrubby	Shrubby	12	48438	LC	moth, bees	birds/bats	Annual	Extended (8)	Annual	Extended (8)
<i>Stetsomia coryne</i> (Salm-Dyck) Britton & Rose	Columnnar	Shrubby	Shrubby	15	36815	LC	moth, bees	birds/bats	Continuous	Extended (11)	Continuous	Extended (11)

fruiting intensity as the frequency at which an individual flowered and fruited. We classified the phenological strategy of each species according to the system developed by Newstrom et al. (1994) as: annual – one flowering/fruitleting cycle within an interval of one year; continuous – flowering/fruitleting throughout the year, with some short intervals (one month) with no reproductive activity; sub-annual – more than one flowering/fruitleting cycle within one year; and supra-annual – flowering/fruitleting events occurring at intervals longer than one year. Likewise, duration of phenophases was classified in brief (1 month), intermediate (2–5 months) or extended (more than 5 months). The degree of overlap between each species' phenophase was assessed using Pianka's index (O_{ijk}) (Pianka, 1973) in EcoSim software (Gotelli and Entsminger, 2000), which ranged from 0 (no overlap) to 1 (complete overlap). Overlap was classified as high (> 0.6), intermediate (between 0.4 and 0.6) or low (< 0.4).

We assayed for seasonal patterns of each species by applying circular statistical analysis as proposed by Morellato et al. (2010). For each phenophase, we calculated the mean angle (μ) and length of the mean vector (r) and performed the Rayleigh test (Z and P). Peak dates were based on the frequency of individuals flowering or fruiting in each month and calculated using Oriana 2.0 software (Kovach Computing Services, Pentraeth, UK). The mean date corresponding to the mean angle (μ) for each phenophase was determined by converting the mean angular directions to corresponding mean dates.

We summed the peak date frequencies at each angle during the two observation years to calculate the average annual flowering and fruiting peak angle or date for each species. We then estimated the value of r (Zar, 1999). The mean angle represented the average data of phenological activity, and r varied from 0 to 1, which indicated the frequency concentration around the mean angle and was considered an index of seasonality if the mean angle was significant (Morellato et al., 2010). The Rayleigh test was used to determine the significance of the mean angle, which verified whether the data was evenly distributed throughout the year (Zar, 1999); if the angle was significant (reject null hypothesis) the pattern was considered seasonal (Morellato et al., 2010).

Multiple linear regressions were used to determine the influence of climatic factors on the number of flowers and fruits produced by each species. Monthly average temperatures and day lengths strongly correlated (Spearman Correlation: $r_s = 0.85$, $p < 0.001$, $n = 24$ months). Thus, because of multicollinearity, we could not use both in the analysis (Neter et al., 1996). Consequently, we regressed the reproductive phenophases in each month against day lengths, relative humidity, and rainfall in the respective month since these variables were more strongly associated with reproductive patterns (higher R^2 values). In accordance with Staggemeir et al. (2010), we refer to day length and temperature in the Discussion to emphasize the correlation between the two variables, even though day length explained more of the variations in cacti phenological responses. To select the simplest and most parsimonious model supported by the data, we selected models based on the information-theoretical approach (Burnham and Anderson, 2002), using the Akaike Information Criterion (AIC) which was performed using R package vegan (R Development Core Team, 2016).

3. Results

Overall, 1198 flowers and 710 ripe fruits ($n = 24$ months) were produced by all cacti species ($n = 10$) in the studied plots. During the two years, at least one cactus species was flowering and/or fruiting in every month (Fig. 2). All species began to bloom during the rainy season when temperatures were higher and the days were the longest. The highest frequency of individuals flowering occurred during the rainy season from November–January, corresponding to months with the longest day lengths (13.21–13.26 h). Fruiting in the cactus community was also more frequent during the rainy season, resulting in peak activity during January (Fig. 2). All species flowered and fruited in



Fig. 1. Flowers and fruits of cacti species studied in the Brazilian Chaco, Porto Murtinho, MS. *Cereus bicolor* (A–L); *Cleistocactus baumannii* (B–M); *Echinopsis rhodotricha* (F–Q), *Frailea schilinzkyana* (J); *Harrisia balansae* (E–P); *Harrisia tortuosa* (D–O); *Opuntia elata* (C–N); *Opuntia retrorsa* (H–S); *Praecereus saxicola* (G–R); *Stetsonia coryne* (I–T). Photo credits: P.R. Souza, B. Ferreira and V. Gomes.

November and December (2014–2015) and between November and January (2015–2016) (Fig. 3).

The species that produced the most flowers were *Stetsonia coryne* (Salm-Dyck) Britton & Rose, *Cleistocactus baumannii* (Lem.) Lem. subsp. *baumannii*, *Echinopsis rhodotricha* K.Schum. subsp. *chacoana* (Schatz) Braun & Esteves with 237, 204, and 146 flowers, respectively. As for fruiting, *S. coryne*, *C. baumannii*, and *Opuntia retrorsa* Speg. were most productive, yielding 104, 103, and 93 fruits, respectively. *Frailea schilinzkyana* (K.Schum.) Britton & Rose subsp. *concepcionensis* (Buining & G.Moser) Braun & Esteves generated the least flowers ($n = 24$) and fruits ($n = 9$) (Fig. 3). The number of flowers was always higher than fruits produced ($U = 16.5$; $p < 0.005$). Significant overlap between flowering frequency and ripe fruits was observed for all species, especially for those in the same genus, including *Harrisia* ($O_{jk \text{ flowering}} = 0.78$; $O_{jk \text{ fruiting}} = 0.88$) and *Opuntia* ($O_{jk \text{ flowering}} = 0.72$; $O_{jk \text{ fruiting}} = 0.81$).

Flowering and fruiting patterns varied from annual to year-round (continuous) (Table 2). In this study, most species displayed annual

flowering and fruiting with extended durations, except for *F. schilinzkyana*, which presented quite intermediate reproductive phenophases. *Stetsonia coryne* and *C. baumannii* showed continuous flowering patterns. Additionally, *S. coryne* was the only species with a continuous fruiting pattern. This species had flowering and fruiting peaks during both the dry and rainy seasons, while all other species displayed a peak during the rainy season (Fig. 3).

Flowering in the community was seasonal ($Z = 384.77$; $p < 0.01$; $r = 0.567$) with mean angle (i.e., mean dates) in December during the rainy season (Fig. 3; Table 2). When analyzing each species separately, only *S. coryne* showed a small degree of flowering seasonality ($r < 0.5$) with a mean date occurring in January, which also occurred during the rainy season (Fig. 3; Table 2). Fruiting within the cactus community also displayed a seasonal pattern ($Z = 234.334$; $p < 0.01$; $r = 0.574$) with a mean angle occurring in January (Fig. 3; Table 2). Again, with the exception of *S. coryne*, all other species had a seasonal fruiting pattern ($r > 0.5$). Among the species that showed seasonality in flowering and fruiting, *Frailea schilinzkyana* showed a high degree of

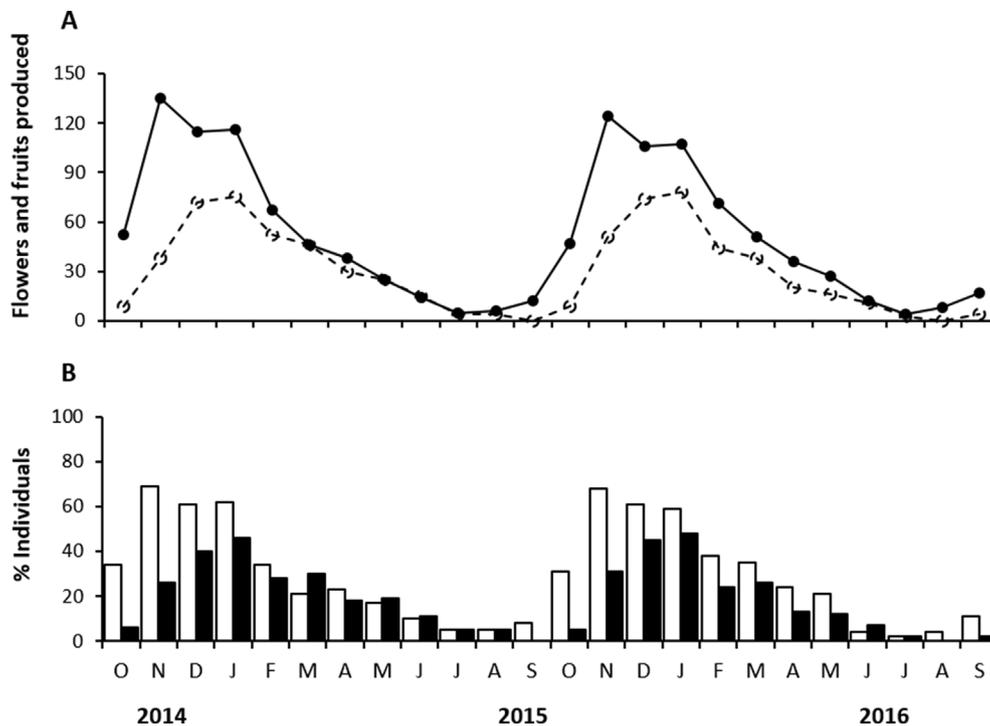


Fig. 2. Flowering and fruiting periods of the cactus community ($n = 10$ species; 138 individuals) from October 2014 to September 2016 in the Brazilian Chaco, Mato Grosso do Sul. A – Flowers (continuous lines) and fruits (dotted lines) produced. B – Percentage of individuals flowering (black bars) and fruiting (gray bars).

seasonal flowering ($r > 0.92$) and fruiting ($r > 0.94$).

The best models related to flowering and fruiting presented few differences between species (Table 3). The timing of flowering among the species was strongly and positively associated with day lengths and temperatures, which explained approximately 83% of the variations in flower production and 78% of the variations in fruit production. Analyzing each species separately, rainfall was not a significant variable in any of the flowering and fruiting models, and relative humidity was only a significant variable for *O. elata* flowering and *S. coryne* fruiting.

4. Discussion

Our results show that cacti species in the Brazilian Chaco respond to environmental conditions with particularly extended reproductive activity. Two species (*C. baumannii* and *S. coryne*) exhibited continuous patterns of flowering and fruiting. Besides *F. schilinzkyana*, the other species showed annual flowering and fruiting patterns with extended durations and reproductive activity during both seasons (*sensu* Newstrom et al., 1994). Such strategy highlights the importance of cacti as a year round resource for local fauna, especially frugivorous fauna. This is particularly significant in the Brazilian Chaco, where abiotic dispersal syndromes are common and few zoochoric fruits are found (Freitas et al., 2013; Carvalho and Sartori, 2014).

We observed a high degree of synchrony between flowering and fruiting, especially for congeneric species. Flowering or fruiting in synchrony could result in an increase of fitness by optimizing pollination and seed dispersal (Staggemeier et al., 2010; Nadia et al., 2012; Gomes et al., 2017). For example, for two *Pilosocereus* species in the Caatinga, frugivorous birds visited and removed seeds more frequently when both cacti species were fruiting (Gomes et al., 2017). This could be seen as a facilitation process, leading to the convergence of phenological timing in plant communities (Elzinga et al., 2007). Conversely, some studies have also suggested that sympatric Cactaceae species tend to displace and avoid overlapping their flowering periods to avoid possible competitive effects, such as reduced reproductive success through competition for pollination, heterospecific pollen flow, and

hybridization (Fleming et al., 1996; Fleming et al., 2001).

The extended flowering activity and high overlap in flowering and fruiting reported in the Brazilian Chaco may be advantageous for cacti species in areas where pollinators are scarce or unreliable. Such strategies could minimize the risks associated with pollination uncertainty and increase the probability of outcrossing (Bawa, 1983; Rathcke and Lacey, 1985). However, the implications of these phenological strategies on plant-animal interactions remain uninvestigated in studies focusing on pollination and seed dispersal in the Brazilian Chaco.

The few phenological studies carried out in the Brazilian Chaco show that reproductive phenological patterns differ from those recorded in other dry and seasonal environments, such as the Caatinga. Carvalho and Sartori (2014) demonstrated a low degree of seasonality with respect to reproductive phenophases in the woody plant community characterized by flowering and fruiting throughout the year with no significant correlations between the phenophases and the climatic variables. Furthermore, Freitas et al. (2013) reported that the community displays continual flowering and fruiting. This study included seven cacti species, which presented their highest reproductive intensities during the rainy season (Freitas et al., 2013). However, phenological patterns may vary at different levels of analyses (Newstrom et al., 1994).

For example, a given species may have its own phenological strategy, which can go undetected when considering the entire community (Boyle and Bronstein, 2012). Although the flowering and fruiting patterns of the Chaco cactus community were seasonal in our study, evaluating the species separately revealed that *S. coryne* had peak flowering and fruiting activities during both the rainy and dry seasons and displayed a low degree of seasonality. In contrast, the other species presented seasonal flowering and fruiting patterns ($r > 0.5$). In particular, *Freilea schilinzkyana* was strongly seasonal ($r = 0.9$), flowering and fruiting for up to 4 and 3 months, respectively.

In addition to intermediate flowering and fruiting periods, *Freilea* produced the fewest flowers and fruits during the study years (24 flowers and nine fruits in total). *Freilea schilinzkyana* is a small globose species that is 4 cm tall and 1.6 cm diameter. This species has limited

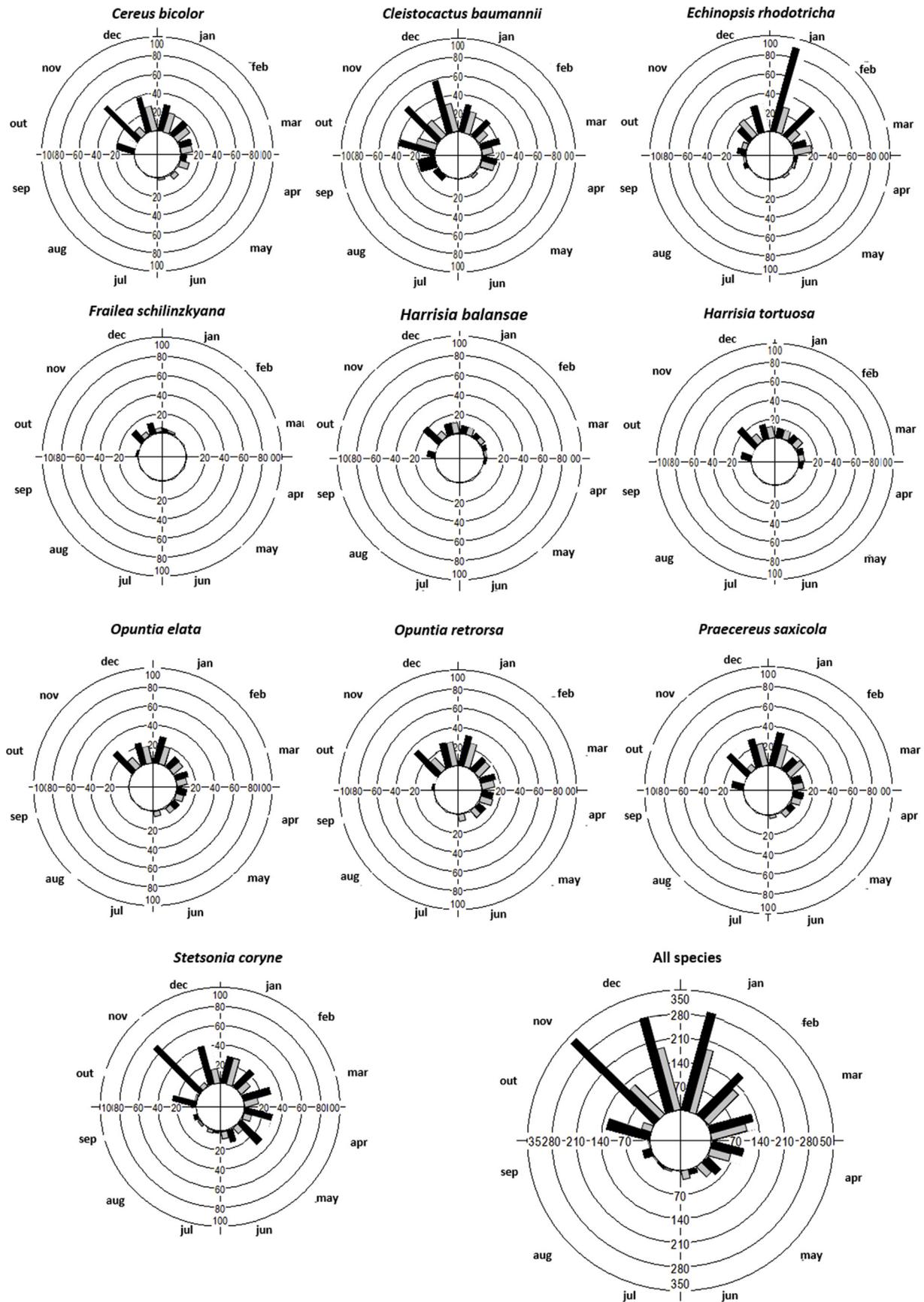


Fig. 3. Circular histograms of flowering (black bars) and fruiting (gray bars) periods of ten cacti species in the Brazilian Chaco, Mato Grosso do Sul. Bars represent the sum of the frequencies of peak dates.

Table 2

Results of circular statistical analysis for the occurrence of seasonality in the reproductive phenological patterns of ten cacti species in the Brazilian Chaco from October 2014 to September 2016. Rayleigh tests were performed to assess the significance of the mean angle (μ).

Species	Flowering						Fruiting					
	(N)	Mean angle (μ)	Mean date	Angular standard deviation	Mean vector (r)	Rayleigh Test (p)	(N)	Mean angle (μ)	Mean date	Angular standard deviation	Mean vector (r)	Rayleigh Test (p)
All species	1198	359,81°	31 Dec	61,06°	0.57	0	710	21,09°	23 Jan	60,32°	0.57	0
<i>Cereus bicolor</i>	136	352,15°	24 Dec	50,04°	0.68	0	92	26,36°	27 Jan	54,28°	0.64	0
<i>Cleistocactus baumannii</i>	204	335,57°	7 Dec	60,85°	0.57	0	103	354,55°	26 Dec	57,94°	0.60	0
<i>Echinopsis rhodotricha</i>	146	10,79°	11 Jan	35,24°	0.83	0	80	14,49°	15 Jan	47,37°	0.71	0
<i>Freilea schilinzkyana</i>	24	329,81°	1 Dec	23,01°	0.92	3.97×10^{-9}	9	331,28°	2 Dec	18,68°	0.95	0
<i>Harrisia balansae</i>	50	343,35°	15 Dec	48,00°	0.70	1.73×10^{-11}	25	4,62°	5 Jan	33,97°	0.84	2.23×10^{-8}
<i>Harrisia tortuosa</i>	64	349,33°	21 Dec	53,37°	0,65	2.13×10^{-12}	34	7,08°	8 Jan	37,55°	0.81	4.74×10^{-10}
<i>Opuntia elata</i>	98	17,34°	18 Jan	57,26°	0.61	0	82	35,37°	4 Feb	64,21°	0.53	7.23×10^{-11}
<i>Opuntia retrorsa</i>	118	15,14°	16 Jan	58,65°	0.59	0	93	35,46°	4 Feb	65,75°	0.52	1.03×10^{-12}
<i>Praecereus saxicola</i>	121	5,86°	6 Jan	57,76°	0.60	0	88	32,37°	2 Feb	57,80°	0.60	0
<i>Stetsonia coryne</i>	237	16,46°	17 Jan	86,70°	0.32	3.76×10^{-11}	104	47,53°	18 Feb	70,94°	0.46	2.38×10^{-9}

Note: bold value = $r < 0.5$ indicating low seasonality; $p = 0$ means that $p < 1.0 \times 10^{-50}$

space for water storage, which differs from other species, such as *S. coryne*. Individuals of *S. coryne* can reach up to 10 m and, in the study area, produced the most flowers and fruits. Higher water storage capacities in large plants allows for better resource allocation for a particular reproductive strategy than smaller plants (Nobel, 2002). Thus, larger plants are expected to be more productive than smaller ones (Godínez-Álvarez et al., 2003; Rojas-Sandoval and Meléndez-Ackerman, 2011).

For cacti species that coexist in the Brazilian Chaco, there seems to be a convergence in reproductive strategies with respect to climatic factors. Despite presenting seasonal patterns with flowering and fruiting peaks in the rainy season, no significant relationship was found between cacti reproduction and rainfall in any of the models. In only one month during the first year (July 2015) and two months during the second year (April and July 2016) was there no rainfall. This opposes the records from the Caatinga, where it is common to see several months without any rain, and rainfall is a limiting factor for the reproduction of some cacti species (Quirino, 2006; Gomes et al., 2014; Gomes et al., 2017).

In tropical regions, seasonality is primarily determined by rainfall, which is considered the main phenological stimulus in seasonal environments, such as the Caatinga (see review in Morelato et al., 2013). In fact, some cacti species from the Caatinga present less extended reproductive phenophases that are strongly correlated with rainfall and have no significant correlation between reproductive phenophases and temperature (e.g. *Cereus jamacaru* DC. subsp. *jamacaru* Gomes et al., 2014; *Pilosocereus* spp. Byles & Rowley Gomes et al., 2017). In a study of five cacti species in the Caatinga, the high variability in phenological patterns was considered a strategy to guarantee reproduction in an environment with erratic rainfall throughout the year (Quirino, 2006). Compared to the Caatinga, the cactus community in the Brazilian Chaco seems to be subject to less seasonal rainfall, but not temperatures. In fact, temperatures in the Chaco vary considerably between seasons, resulting in the highest absolute values for South America during the rainy season, when it reaches 49 °C (Prado, 1993), contrasting with occasional frosts during the winter.

Unlike the Caatinga, the seasonal pattern recorded in the Chaco is best explained by day length and temperature, since the longest and warmest days occur during the rainy season and the flowering and fruiting peaks overlap with the longest day lengths (November to January) when temperatures are also higher (Fig. 2B and Fig. S2). Many tropical forest species are sensitive to changes in temperature and day length, and flowering and fruiting in the most favorable period

correspond to the transition from the dry season to the rainy season and during the rainy season proper (Morellato et al., 2000; Staggemeier et al., 2010).

Seasonal variation in day length is the only consistent environmental signal from year to year and is independent from seasonal and inter-annual variation in climate. Day length can induce synchronous phenology in conspecific trees at the same time every year (Borchert et al., 2005). During the two years of phenological monitoring, the cacti species were sensitive to changes in temperature and day length, which correlated with changes in flowering and fruiting dynamics during the longest and warmest days. In an area of dry Chaco in Argentina, flowering and fruiting activities intensified during sunnier periods (Marco and Paéz, 2002). According to Marco and Paéz (2002), the seasonal patterns of solar irradiation and rainfall, which are positively correlated, provide conditions that trigger the phenological activities of the species studied. Nevertheless, different results were observed for *Harrisia portoricensis* Britton on Mona Island (Rojas-Sandoval and Meléndez-Ackerman, 2011), which displayed reproductive phenological patterns that did not correlate with day length.

In tropical rain forests, where water stress and extreme variations in temperature are absent, day length is considered a reliable cue that triggers the timing and synchronization of flowering (Wright and van Schaik, 1994; Morellato et al., 2000). Considering the model results, a high variability in temperatures throughout the year, as well as a positive correlation between this variable and day length, suggest that shifts in day length and temperature are the main phenological stimulus shaping broad reproductive patterns in cacti species in the Brazilian Chaco. Therefore, we emphasize the importance of considering other climatic factors, such as irradiance, day length and humidity, besides rainfall and temperature in phenological studies of this family.

In the Brazilian Chaco, cacti species are subject to different pollination and seed dispersal syndromes involving ants, bees, bats, moths, hummingbirds, and birds (see Gomes and Araujo, 2015; and Table 1). Most species present flowers with attributes related to nocturnal pollination (*Cereus bicolor* Rizzini & A. Mattos, *Echinopsis rhodotricha*, *Harrisia balansae* (K.Schum.) N.P. Taylor & Zappi, *Harrisia tortuosa* (J.Forbes ex Otto & A.Dietr.) Britton & Rose, *Praecereus saxicola* (Morong) N.P. Taylor and *Stetsonia coryne*), which is likely performed by moths and bats, however, these species had low visitation frequencies, almost exclusively by secondary pollinators (Ferreira et al., 2018; unpublished data VGN Gomes). One exception is *Cleistocactus baumannii*, which is exclusively visited by hummingbirds (Gorostiague and Ortega-Baes, 2015). Thus, we suggest that the extended

Table 3
Akaike Information Criterion (AIC) between rainfall, day length and relative humidity and reproductive phenophases of ten cacti species from the Brazilian Chaco from October 2014 to September 2016. Δ AIC = initial AIC - final AIC. Number of observations = 24 months.

Species	Flowering						Fruiting									
	Δ AIC	Intercept	r ²	F	P	Rainfall	Day length	Humidity	Δ AIC	Intercept	r ²	F	P	Rainfall	Day length	Humidity
All species	1,41	-330,48	0,83	42,03	4,55 × 10 ⁻⁸	-	23,03***	-	1,43	-367,53	0,78	59,74	2,15 × 10 ⁻⁹	0,18 NS	33,77***	-
<i>Cereus bicolor</i>	1,30	-47,37	0,61	19,32	1,73 × 10 ⁻⁵	-	3,37***	-	1,32	-47,76	0,71	30,1	6,80 × 10 ⁻⁷	0,03 NS	4281***	-
<i>Cleistocactus baumannii</i>	3,42	-39,22	0,72	60,46	9,43 × 10 ⁻⁸	-	3,65***	-	2,58	-63,13	0,60	36,78	4,19 × 10 ⁻⁶	-	6,02***	-
<i>Echinopsis rhodortricha</i>	2,75	-36,61	0,56	30,99	1,35 × 10 ⁻⁵	-	3,35***	-	1,97	-83,92	0,53	27,04	3,25 × 10 ⁻⁵	-	7,56***	-
<i>Frailea schilitzkyana</i>	1,98	-2,88	0,26	5,09	0,01	0,004 NS	0,24**	-	1,98	-8,55	0,32	6,47	0,006	0,008 NS	0,74*	-
<i>Harrisia balansae</i>	3,16	-14,24	0,72	60,53	4,34 × 10 ⁻⁸	-	1,285***	-	1,90	-16,61	0,51	13,23	0,001	0,01 NS	1,49***	-
<i>Harrisia tortuosa</i>	1,83	-21,71	0,77	41,51	5,05 × 10 ⁻⁸	-	1,66***	-	1,51	-21,06	0,58	17,08	3,94 × 10 ⁻⁵	0,01 NS	1,91***	-
<i>Opuntia elata</i>	0,11	-32,25	0,65	15,5	1,90 × 10 ⁻⁵	-	1,76***	0,16*	1,00	-30,03	0,69	26,68	1,71 × 10 ⁻⁶	0,02 NS	2,71***	-
<i>Opuntia retrorsa</i>	0,63	-43,21	0,59	18	2,80 × 10 ⁻⁵	-	2,32***	-	0,69	-35,59	0,71	29,48	8 × 10 ⁻⁷	0,02 NS	3,323***	-
<i>Praceereus saxicola</i>	1,90	-43,04	0,66	24,24	3,50 × 10 ⁻⁶	-	2,92***	-	0,74	-41,23	0,75	36,5	1,46 × 10 ⁻⁷	0,01 NS	3,76***	-
<i>Stetsonia coryne</i>	1,48	-34,55	0,42	9,59	0,001	-	1,94**	-	0,25	-41,77	0,52	9,49	0,001	0,05 NS	2,13***	0,28*

Note: Statistical significance (*p < 0,05; **p < 0,01; ***p < 0,001; NS indicates that the regression coefficient is not significant).

phenological patterns and high overlap in flowering and fruiting reported here may be related to the occurrence of more generalist pollination systems in the study area, which appear to be more common for Cactaceae than previously thought (see Gorostiague and Ortega-Baes, 2015, 2017).

Finally, the flowering and fruiting patterns (seasonal, annual, or continuous with an extended duration) of the cactus species from the Brazilian Chaco provide resources for fauna throughout the year, and may also be a strategy to maintain pollinator and seed disperser populations, which ensures the reproductive success of these plants. However, studies evaluating pollination and seed dispersal interactions should be conducted to confirm such conclusions since high flowering and fruiting overlap could result in either competitive or facilitative effects.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jaridenv.2018.11.001>.

Note: Annual: one flowering cycle (some months of flowering followed by a period without flowers) at an interval of one year; Continuous: flowering throughout the year, but there can be some short intervals (one month) without flowering; Brief (1 month), Intermediate (2–5 months) or Extended (more than 5 months).

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