



Endangered globose cactus *Melocactus lanssensianus* P. J. Braun depends on lizards for effective seed dispersal in the Brazilian Caatinga

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Abstract Effective seed dispersal is essential to plant reproductive success. In this study, we evaluated the fruiting phenology, fruit traits, and seed dispersal of the endangered globose cactus *Melocactus lanssensianus* in the Brazilian Caatinga over 1-year period. We carried out monthly phenological monitoring, focal observations, and germination experiments, to identify the effective seed dispersers of this cactus. *M. lanssensianus* exhibited a continuous, non-seasonal fruiting pattern, with peaks during both the dry and rainy seasons. We observed seed dispersal by *Tropidurus semitaeniatus* and *T. hispidus* lizards. In 116 h of focal observations, lizards made 76 visits during different times of day, with a mean dispersal distance of 5 m. Both lizard species showed more frugivory interactions in the dry season, with peak visits in

water-stressed months. We collected 132 intact and viable seeds from 29 fecal samples, specifically from *T. semitaeniatus* ($N = 20$ scats; 122 seeds) and from *T. hispidus* ($N = 9$ scats; 10 seeds). Germination experiments with seeds consumed by *T. semitaeniatus*, washed seeds and control seeds revealed that 85% of seeds found in *T. semitaeniatus* feces germinated compared to 41% of the control seeds. Frequency, pattern of visits and germination rates indicate *T. semitaeniatus* is an effective seed disperser of *M. lanssensianus*. Continuous production of fleshy fruits and environmental conditions of the Caatinga ecosystem favor the close dependent mutualistic interaction reported here.

Keywords Cactaceae · Fruiting phenology · Germination · Saurochory · Seasonality

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Introduction

Cactaceae is one of the most diverse families in the Neotropics, with 1480 recognized species (Goettsch et al. 2015) and Eastern Brazil ranks third worldwide for cacti diversity (Taylor and Zappi 2004). In the Brazilian Caatinga, the largest tropical dry forest region in South America (Silva et al. 2017), Cactaceae constitute an important floristic element with 99 species and 25 genera (Zappi and Taylor 2020). In

this seasonal ecosystem, cacti species are widely recognized for their ecological role (e.g., continuous production of flowers and fruits; mutualistic interactions with pollinators and seed dispersal by a wide range of animals) (Quirino 2006; Gomes et al. 2014a,b; Gomes et al. 2016, 2017; Rocha et al. 2019; Santos et al. 2019).

Seed dispersal mutualism is a key ecological process in plant reproductive success and maintenance of biodiversity (Schupp et al. 2010; Andresen et al. 2018). Endozoochory is a dispersal mode that consists of fruit consumption by animals followed by the liberation of viable seeds in their fecal samples (Fenner and Thompson 2005). It occurs widely among cacti species (Fleming and Valiente Banuet 2002; Mandujano et al. 2010; Gomes and Araujo 2015). Cactus fleshy fruits contain a succulent funicular pulp and have a variety of shapes, scents, and colors for attracting diverse frugivores, including birds, lizards, ants, non-flying mammals, and bats (Taylor and Zappi 2004). Such frugivores can be effective seed dispersers, with effectiveness assessed by quantitative and qualitative components including frequency, dispersal distance, seed germination after passage through the digestive tract and seed deposition site (Schupp et al. 2010; González-Castro et al. 2015).

Saurochory refers to seed dispersal by lizards and other reptiles, especially on oceanic islands (Valido and Olesen 2007, 2019). In arid and semiarid continental areas of the Neotropical region, studies have reported lizard interactions with cacti, including globose (e.g., Nassar and Ramírez 2004; Casado and Soriano 2010; Fonseca et al. 2012; Gomes et al. 2014b; Xavier and Dias 2017) and columnar species (Gomes et al. 2016, 2017; Paixão and Venticinque 2020; Silva et al. 2021a,b; Sousa Neto et al. 2021). In the cactus genus *Melocactus* Link & Otto, saurochory is classified as a facultative positive interaction (Guerrero et al. 2012). Some characteristics of *Melocactus* spp., such as globose plant growth near to the ground with fleshy and colorful berry fruits, facilitate detection and fruit consumption by lizards that might act as seed dispersers (Vasconcellos-Neto et al. 2000). However, few studies have addressed the effectiveness of lizard species as seed dispersers (e.g., Figueira et al. 1994; Fonseca et al. 2012; Guerrero et al. 2012; Gomes et al. 2014b).

Melocactus lanssensianus P. J. Braun (1986) is a globose cactus endemic to granitic outcrops of the

Caatinga ecoregion (Taylor and Zappi 2004; Machado et al. 2013). This species is classified as endangered (EN) on IUCN Red List and loss of habitat quality is its greatest threat (Braun and Taylor 2013). Due to their high ornamental potential and easy removal from the field, several *Melocactus* spp. are traded illegally, leading them to appear on the Red List of Brazilian Flora (Martinelli et al. 2013; Cardoso et al. 2018; Caitano et al. 2020). According to the Brazilian Red List, *M. lanssensianus* is categorized as endangered. Therefore, studies addressing reproductive ecology are vital to support conservation action for this endangered cactus (Machado et al. 2013).

In this study, we evaluate fruiting phenology, fruit traits, and seed dispersal of *M. lanssensianus* in the Brazilian Caatinga over 1-year period. We recorded frequency of frugivore visits and their dispersal distance, and then tested their effectiveness as seed dispersers by assessing the effect of passage through the digestive tract on germination success of seeds.

Material and methods

Study site

Our study site was the Pão de Açúcar Ranch, a private property (06°35'27.8" S and 35°27'39.5" W) located in the Agreste Paraibano mesoregion, Tacima municipality, Paraíba state (Brazilian Semiarid region) (Fig. 1A, B). The Pão de Açúcar Ranch has 200 ha dominated by Caatinga vegetation and three granitic outcrops ≥ 500 m from each other (Fig. 1C, D). These are located at 233 m above sea level and the highest is 108 m high (Lima 2018). The granitic outcrops are characterized by the presence of a discontinuous shrub layer containing thorny and microphyllous species, as those in Fabaceae, Bromeliaceae, and Cactaceae. Three cacti species occur in this area, *Cereus jamacaru* D.C., *Xiquexique gounellei* (F.A.C. Weber) Lavor & Calvente, and *Melocactus lanssensianus* P.J. Braun.

Fieldwork was conducted monthly from May 2020 to April 2021 in the two lower granitic outcrops. Fieldwork in the highest outcrop found no reproductive individuals of *M. lanssensianus* and thus was no further fieldwork was done on this outcrop. The climate of the study area is classified as warm and humid with rainy winter, “As” according to the

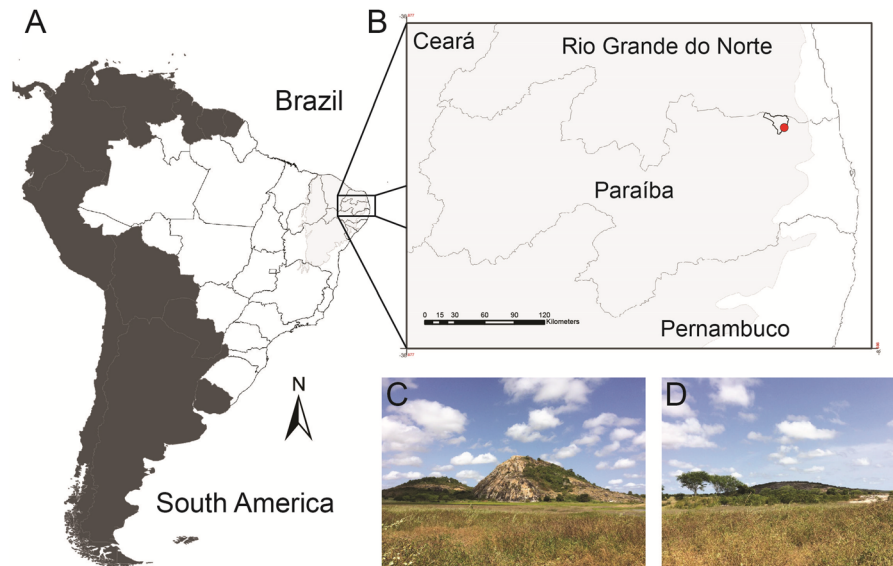


Fig. 1 A Map of South America (dark gray) highlighting the geopolitical division of Brazil (white) and Caatinga region (soft gray); B Paraíba state highlighting Tacima municipality.

Localization of sampling area at Pão de Açúcar Ranch (red circle) composed of three granitic outcrops (C–D)

Köppen system (Alvares et al. 2013). The region has irregular rainfall (600 mm/year), short rainy season (March to June), long periods of drought, and high average annual temperature varying from 25° to 30 °C (Souza et al. 2018). During the period of data collection, average annual rainfall and temperature were 655 mm and 28.6 °C, respectively.

Studied species

Melocactus lanssensianus is a depressed-globose cactus, popularly known as “coroa-de-frade”, reaching 14 cm in high. It occurs exclusively in three localities of Pernambuco and Paraíba states (Braun 1986; Taylor and Zappi 2004; Machado et al. 2013). Taxonomic studies suggest that *M. lanssensianus* produces cleistogamous flowers that are not exposed on the cephalium surface (Braun 1986; Taylor 1991; Taylor and Zappi 2004). The pink flowers remain inside the cephalium, forming dry floral remains (6 mm in length) attached to the fruit (Taylor and Zappi 2004). Fruits are claviform-shaped and pink-colored berries, with black seeds embedded in the funicular pulp (Braun 1986; Taylor 1991; Taylor and Zappi 2004). Voucher specimens of *Melocactus lanssensianus* were deposited in the Herbarium Lauro

Pires Xavier at the Department of Botany, Federal University of Paraíba (JPB – 66234).

Both *Tropidurus semitaeniatus* Spix, 1825 and *Tropidurus hispidus* Spix, 1825 are omnivorous and heliothermic lizards. *T. semitaeniatus* is 20 cm in total length and *T. hispidus* reach up to 35 cm in total length, the largest of the genus (Kolodiuk et al. 2010). *T. semitaeniatus* is endemic to rocky habitats in the Caatinga of northeastern Brazil where it occurs in sympatry with several congener species (Ribeiro and Freire 2011; Passos et al. 2011). *T. hispidus* occurs in several types of open habitats in South America, with a continuous distribution in both Caatinga and coastal areas of northeastern Brazil, living in forest borders, rocky outcrops, and human-altered areas (Fialho et al. 2000; Carvalho 2013).

The generalist diet of both species includes invertebrates and plant material, such as leaves, flowers, fruits, and seeds (Cooper Jr and Vitt 2002; Ribeiro et al. 2008); and *T. hispidus* also consumes vertebrates (Vitt 1995; Van Sluys et al. 2004; Kolodiuk et al. 2010; Ribeiro and Freire 2011; Albuquerque et al. 2018). Previous studies have reported the fruit consumption of globose and columnar cacti species by *T. semitaeniatus* (Fonseca et al. 2012; Gomes et al. 2014b, 2016; Silva et al. 2021b), and flower and fruit consumption of columnar species by *T. hispidus*

(Gomes et al. 2017; Paixão et al. 2021; Sousa Neto et al. 2021).

Fruiting phenology and fruit traits

Phenological monitoring was conducted in the field monthly from May 2020 to April 2021, by directly counting fruits of 15 adult individuals, growing separated by at least 10 m. The fruits were counted to estimate resource availability for seed dispersers. Fruiting descriptors were analyzed (number of fruits produced and number of fruiting plants) using the system developed by Newstrom et al. (1994). We assayed for seasonal patterns of fruiting by applying circular statistical analyses as proposed by Morellato et al. (2010). The mean vector or mean angle (μ), length of the mean vector (r), and Rayleigh test (Z and p) (Zar 2010) were calculated using the Oriana 2.0 software (Kovach Computing Services, Pentraeth, UK, 2004). The mean angle corresponds to mean date of phenophase and r indicates the frequency concentration (synchronization) around the mean date (Morellato et al. 2010). High r values (> 0.5) implies aggregate phenological activity around the mean date. There are seasonality when Z values are significant ($p < 0.05$).

Spearman's rank correlation tests were used to assess the relationship between fruiting descriptors and climatic variables. Monthly meteorological data (rainfall and temperature) from a local weather station, made available by the Agência Executiva de Gestão das Águas do Estado da Paraíba (AESAs) and Instituto Nacional de Meteorologia (INMET), were obtained.

One fruit from each of 30 *M. lanssensianus* individuals was collected and analyzed. For each fruit, we recorded the color, type of dehiscence, and number of seeds present (Pijl 1982). We recorded the time of appearance of fruits on the surface of the cephalium. A digital caliper and precision scale were used to record length, width, and weight of both fruits and seeds. We measure fruit wet weights before drying, then fruit dry weights were obtained after drying fresh fruits at 70 °C for 24 h to estimate the moisture content (%) according to the Official Methods of Analysis (AOAC 2000). Brix concentration of the funicular pulp was measured using a digital refractometer. All fruit and seed traits were analyzed at the Laboratory of Cultivo in the National Institute of Semiarid (INSA).

Fruit visitors

To assess interactions with lizards, we did focal observations monthly on 15 individuals of *M. lanssensianus* on non-consecutive days from May 2020 to April 2021, corresponding to the whole period of phenological monitoring. Each session of focal observations lasted 1 h, interpolated with 30-min intervals, totalling 116 h of focal observation. We recorded the frequency of visits, time spent on the cephalium and behavior of visitors toward fruits between 7:00 and 17:00 h. All focal observations were made at approximately 5 m from the focal plant and were complemented with video and photographic records. This distance was chosen to minimize any possible observer influence on the behavior of animal visitors. We used the same circular statistics as those used for fruiting data to evaluate the occurrence of seasonal variation in the number of fruit visits.

Germination experiments

The effect of passage through the digestive tracts of lizards on seeds was experimentally investigated. Three germination treatments were considered: seeds consumed by *T. semitaeniatus* ($N = 20$ scats; 122 seeds) that were collected from fecal samples at different distances from the closest reproductive adult cactus; seeds manually washed for 2 min to remove funicular pulp; and a control of seeds directly removed from different fruits (not washed or consumed). The last two treatments had 100 seeds in each. Seeds were randomly collected from fruits of ten different *M. lanssensianus* individuals. The lizard *T. hispidus* was excluded from germination experiments due to the low number of seeds obtained in their fecal samples. We analyzed consumed seeds with a stereomicroscope and used the seed collection of the Cactarium Guimarães Duque in the National Institute of Semiarid as reference to identify seeds.

Germination tests were conducted under 30 °C and 12 h photoperiod (Meiado et al. 2016). We repeated each treatment four times using 25 seeds on Petri dishes containing filter paper moistened with 5 ml of the distilled water. The dishes were sealed with transparent masking tape. No additional water was added and no fungi contaminations were observed during the monitoring period ($N = 30$ days).

Germination was defined as protrusion of the radicle ≥ 1 mm from the seed coat (Meiado et al. 2010).

At the end of the experiments, we evaluate germination parameters, germinability (arcsine $\sqrt{\%}$), and mean germination time [$t = \sum ni.ti / \sum ni$, in which ti is the time since the onset of the experiment to the n th observation (days) and ni is the number of seed germinated in time i (not the accumulated number, but the number corresponding to the n th observation)] based on Ranal and Santana (2006). Differences in germination parameters among treatments were tested for statistical significance using a one-way ANOVA followed by a Tukey's honestly significant difference test. The normal distribution of the data and homogeneity of the variances were tested using Shapiro–Wilk and Levene tests, respectively. Statistical analyses were performed using vegan package (Oksanen et al. 2018) in R programming (R Development Core Team 2017).

Results

Fruiting phenology and fruit traits

M. lanssensianus produced fruit in all months of phenological monitoring, with the 15 monitored individuals producing a total of 256 fruits. Fruit production peaked during both the dry (October) and rainy (March) seasons (Fig. 2). Each cactus produced on average 1.42 fruits per sample day (ranging 1–4 fruits per individual) (Fig. 3A). The fruiting pattern was continuous (sensu Newstrom et al. 1994) and non-seasonal ($r < 0.5$; $p > 0.05$). The mean dates occurred in August (fruiting individuals) and November (number of fruits) (Table 1). No significant correlations were found between fruiting and climatic variables (rainfall $rs = 0.1188$; $p = 0.7128$; temperature $rs = 0.2028$; $p = 0.5273$). During the phenological monitoring, there was no record of either flowers or buds of *M. lanssensianus* on the cephalium surface, confirming cleistogamy.

Fruits of *M. lanssensianus* appeared gradually on surface of the cephalium at around 09:00–10:00 h. The time interval between appearance and complete expulsion of each fruit on the cephalium surface was 20 ± 2.0 min. The fruits were claviform berries, bright lilac in color, indehiscent, 17.04×8.4 mm long, and weighing 0.3208 mg (Table 2; Fig. 3B).

Each one held, on average, 38 ± 14 black seeds, embedded in an aqueous translucent pulp. Seed size was 1.03×1.01 mm with a weight 0.02 mg. The moisture content of fruits and pulp brix concentration were $85.3\% \pm 1.5$ and $8.0\% \pm 1.16$, respectively.

Fruit visitors

M. lanssensianus individuals were visited by two lizard species. In 116 h of focal observation, 76 interactions were recorded, 58 with *T. semitaeniatus* and 18 with *T. hispidus* (Table 3). *T. semitaeniatus* was the most frequent frugivore visitor (0.50 visits h^{-1}) and visited in all months of monitoring, while *T. hispidus* (0.15 visits h^{-1}) was observed consuming fruit in only two months. The visits of both species peaked in frequency during the dry season (Fig. 2). Circular statistical analyses found non-seasonal ($r < 0.5$) and seasonal ($r = 0.783$) patterns of visits in *T. semitaeniatus* and *T. hispidus*, respectively. The mean dates of visits occurred in September (*T. semitaeniatus*) and December (*T. hispidus*) (Table 1).

Visits of *T. semitaeniatus* varied with time of day, with 60% of frugivory interactions concentrated right after fruit exposure (around 10:00 h). *T. semitaeniatus* individuals showed two types of behavior when accessing the fruits of *M. lanssensianus*: 1) climbing (Fig. 3C) or 2) jumping directly on the cephalium surface of the cactus (Fig. 3D, E). Visits lasted an average of 40 ± 21 s. Fruit consumption occurred on top of the cephalium or to the side of the plant. The lizards rotate the fruit multiple times, making several attempts until they can swallow it completely (Online Resource 1).

More juvenile ($N = 43$ records) than adult ($N = 15$ records) visits of *T. semitaeniatus* were observed. Sometimes, the same individual lizard made consecutive visits and consumed all exposed fruits on the cephalium. On two occasions, we recorded agonistic interactions and fights between adults and juveniles vying for fruits. In one of these observations, an adult lizard visited a plant with two exposed fruits. As it bit into the first fruit while next to the plant, a juvenile lizard came and took the other fruit. The adult immediately chased this juvenile lizard and picked up the other fruit (Online Resource 2).

Frugivory interactions of *T. hispidus* occurred between 12:00 and 17:00 h and all were juveniles ($N = 18$ records). *T. hispidus* ate the fruit in a bipedal

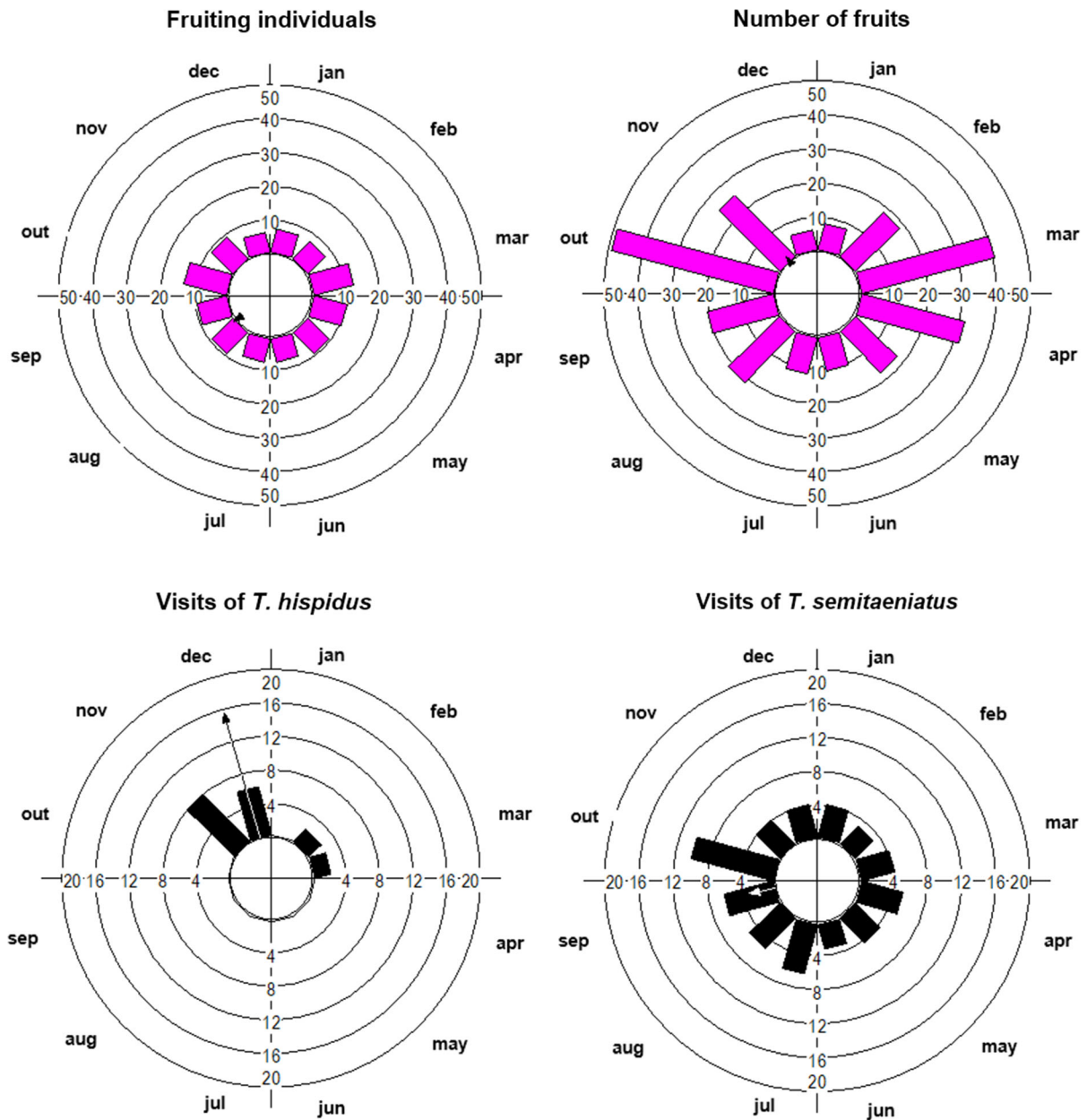


Fig. 2 Circular histograms of fruiting phenology and visits of *Melocactus lanssensianus* throughout the year in the Pão de Açúcar Ranch, Tacima municipality, Paraíba state, northeastern Brazil from May 2020 to April 2021. Letters around the circle

indicate the months and bars inside the histograms indicate the number of fruiting individuals, fruits and visits in the respective month

position without climbing on the cephalium surface. Its visits lasted about 20 ± 4 s, from arrival at the cactus until complete ingestion of the fruit in a single bite. In one of these visits, *T. hispidus* consumed only half of the fruit, discarding the other half, in which eight seeds remained in the funicular pulp.

Fecal samples and germination experiments

We collected 29 fecal samples of both lizard species at an average distance of 5 m from the closest reproductive adult cactus (Table 3). We collected 132 intact and viable seeds from fecal samples, specifically, *T.*

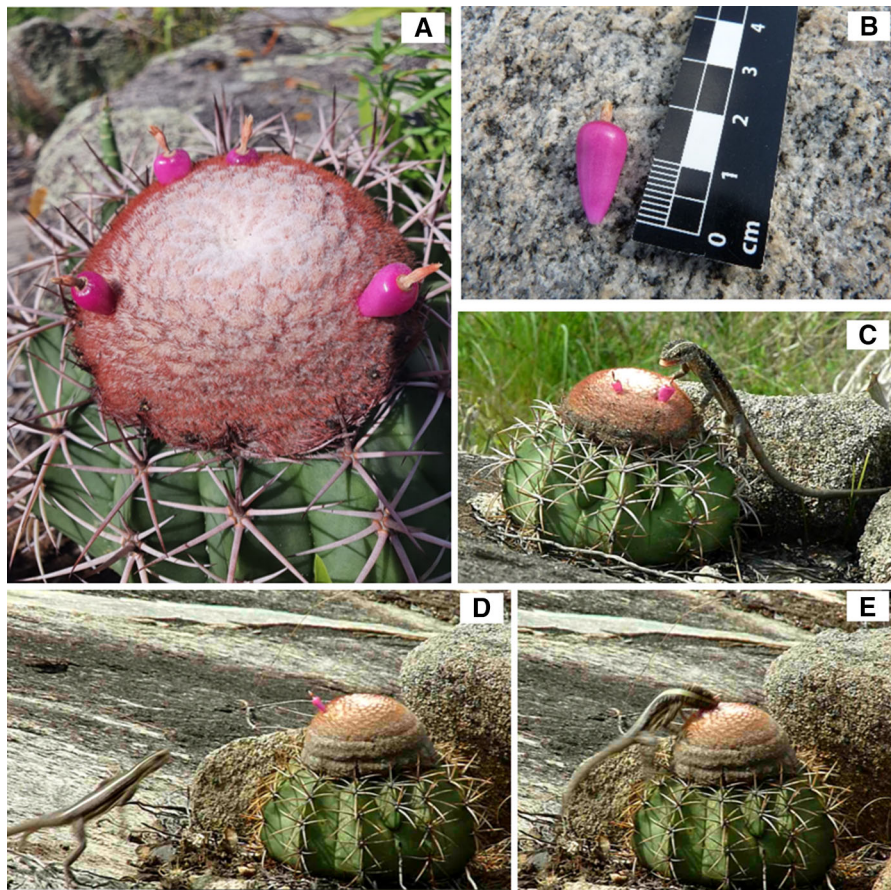


Fig. 3 **A** *Melocactus lanssensianus* individual exposing fruits on the surface of the cephalium; **B** Claviform-shaped fruit of *M. lanssensianus*; *T. semitaeniatus* individuals climb **C** and jump **D**, **E** on the cephalium surface and consuming fruits of *M.*

lanssensianus. All pictures were taken in an area of granitic outcrop in the Pão de Açúcar Ranch, Tacima municipality, Paraíba state, northeastern Brazil

Table 1 Results of circular statistical analyses of fruiting phenology of *Melocactus lanssensianus* and frequency of visits by *Tropidurus hispidus* and *Tropidurus semitaeniatus* in the

Pão de Açúcar Ranch, Tacima municipality, Paraíba state, northeastern Brazil from May 2020 to April 2021

Data	N	μ	Mean date	μ (SD)	r	Z	p
Fruiting individuals	105	234.399	26 aug	167.851	0.014	0.02	0.981
Number of fruits	256	319.788	21 nov	148.873	0.034	0.299	0.741
Visits of <i>T. hispidus</i>	18	343.898	15 dec	40.092	0.783	11.031	0.0001
Visits of <i>T. semitaeniatus</i>	58	259.844	21 sep	109.951	0.159	1.459	0.232

Bold value = $r > 0.5$ indicating seasonality

Number of observations throughout the year (N), mean vector (μ), mean date, mean vector standard deviation (SD), mean vector length (r), and Rayleigh test (Z and p)

semitaeniatus (N = 20 scats; 122 seeds) and *T. hispidus* (N = 9 scats; 10 seeds). For *T. semitaeniatus*, all scat contained seeds, with an average of 6

seeds scat⁻¹. In *T. hispidus*, 10 seeds were present in one of nine scat samples. We also found seeds of *X.*

Table 2 Fruit and seed traits of *Melocactus lanssensianus* ($N = 30$) in the Pão de Açúcar Ranch, Tacima municipality, Paraíba state, northeastern Brazil

Traits	<i>M. lanssensianus</i>
Fruit size (mm)	
Length	17.04 ± 1.5
Width	8.4 ± 0.8
Seed size (mm)	
Length	1.03 ± 0.01
Width	1.01 ± 0.01
Weight (mg)	
Fruit	0.320 ± 0.10
Seed	0.02 ± 0.01
Moisture content (%)	85.3 ± 1.16
Brix (%)	8.0 ± 1.5
Number of seeds	38 ± 14

Data are mean ± SD

Table 3 Visits by lizards on fruits of *Melocactus lanssensianus* in the Pão de Açúcar Ranch, Tacima municipality, Paraíba state, northeastern Brazil from May 2020 to April 2021

Visits	<i>T. hispidus</i>	<i>T. semitaeniatus</i>
Number of visits	18	58
Frequency (visit.h ⁻¹)	0.15	0.50
Duration of visits (seconds)	20 ± 4	40 ± 21
Fecal samples (n)	9	20
Seeds in fecal samples (n)	10	122
Mean dispersal distance (m)	5.8 ± 3.0	5.1 ± 1.5

gounellei ($N = 14$ seeds) in three scat samples from *T. semitaeniatus* in March.

Passage through the digestive tract of *T. semitaeniatus* increased the germination rate of *M. lanssensianus* seeds (Table 4). In the germination experiments, consumed seeds had significantly higher germinability than control seeds ($p < 0.00001$). Nearly 85% of seeds found in the lizards feces germinated, in contrast with 41% in the control treatment. The highest germinability was observed for washed seeds (90.5%) but the difference in germination between washed seeds and those consumed by lizards was not statistically significant (Table 4). We also observed a significantly lower mean germination time in washed seeds ($t = 7.21 \pm$

Table 4 Germinability (%) and mean germination time (MGT) of *Melocactus lanssensianus* seeds germination (control), consumed and washed seeds by *Tropidurus semitaeniatus* in the Pão de Açúcar Ranch, Tacima municipality, Paraíba state, northeastern Brazil

Treatment	G (%)	MGT
Control	41.0 ± 6.0 ^c	10.5 ± 0.3 ^a
Consumed seeds	85.0 ± 2.5 ^b	7.51 ± 0.2 ^b
Washed seeds	90.5 ± 3.0 ^{ab}	7.21 ± 0.3 ^b

Data are mean ± SD

Different letters indicate significant differences at $p < 0.05$

0.3 days) and consumed seeds ($t = 7.51 \pm 0.2$ days) compared to the control seeds ($t = 10.5 \pm 0.3$ days).

Discussion

M. lanssensianus has characteristics associated with saurochory, including growth near the ground, facilitating access to fleshy, colorful, and claviform-shaped fruits on the cephalium and this study confirms *Tropiduridae* lizards are its exclusive seed dispersers. Two species of *Tropidurus* were recorded interacting with fruits of *M. lanssensianus*, however, some particularities were observed during the visits of each lizard species and species differed in frequency, pattern of visits and number of seeds found in fecal samples.

Both *Tropidurus* species provide seed dispersal, ingesting and defecating intact seeds away from parent plants. Of the two lizard species we observed, we conclude that *T. semitaeniatus* is an effective seed disperser given their consistent pattern of visits throughout the year and the increased germination rate of seeds that passed through its digestive tract. *T. hispidus* is a less regular visitor with a complementary role in the seed dispersal of *M. lanssensianus*. More than 75% of frugivory interactions were carried out by *T. semitaeniatus* and 24% by *T. hispidus*. Moreover, *T. semitaeniatus* visited fruits in all sampling months with a frequency of visits three times higher compared to *T. hispidus*. The mean dispersal distance of 5 m was similar for *T. hispidus* and *T. semitaeniatus*, but the number of seeds in fecal samples differed between lizard species. We found more than a hundred intact

seeds in the fecal samples of *T. semitaeniatus*, but only ten seeds in a single scat sample from *T. hispidus*.

In Brazil, frugivory and diet studies have recorded consumption of *Melocactis* fruits by lizards and commonly by *Tropidurus* spp. Examples in the Restinga sandy coastal plains include *Melocactus violaceus* Pfeiff. + *Tropidurus torquatus* Wied-Neuwied, 1820 (Figueira et al. 1994); *M. violaceus* + *T. hygomi* Reinhardt & Lütken, 1862 (Xavier et al. 2015a); *M. violaceus* subsp. *margaritaceus* N.P. Taylor + *Glaucmastix abaetensis* Dias, Rocha & Vrcibradic, 2002 (Xavier et al. 2015b). Examples in the Caatinga tropical dry forest include *M. glaucescens* Buining & Brederool *M. paucispinus* Heimen & R.J. Paul + *T. cocorobensis* Rodrigues, 1987/ *Ameivula ocellifera* Spix, 1825 (Fonseca et al. 2012); *M. ernestii* Vaupel subsp. *ernestii* + *T. semitaeniatus* (Gomes et al. 2014b); *M. zehntneri* (Britton & Rose) Luetzelb. + *T. pinima* Rodrigues, 1984 (Xavier and Dias 2017). In semiarid and arid areas in Venezuela, interaction records include *M. schatzlii* H. Till & R. Gruber + *Ameiva provिताе* Garcia-Perez, 1995/ *Cnemidophorus lemniscatus* Linnaeus, 1758 (Casado and Soriano 2010); *M. curvispinus* Pfeiff. + *A. bifrontata* Cope, 1862/ *C. senectus* Ugueto, Harvey & Rivas, 2010/ *T. hispidus* (Guerrero et al. 2012). Some of these studies evaluated seed passage through the *Tropidurus* digestive tract and found increased germinability [*M. violaceus* + *T. torquatus* (Figueira et al. 1994); *M. ernestii* subsp. *ernestii* + *T. semitaeniatus* (Gomes et al. 2014b)], while others found germination rates were unaffected [*M. glaucescens*/ *M. paucispinus* + *T. cocorobensis* (Fonseca et al. 2012); *M. curvispinus*/ *M. schatzlii* + *T. hispidus* (Guerrero et al. 2012)].

Our findings reveal that seeds consumed by *T. semitaeniatus* and washed seeds have better germinability than do seeds with fruit pulp still present (control). Removal of funicular pulp led to an increase of 45% in the germinability of *M. lanssensianus*. In addition, consumed and washed seeds germinated 3 days earlier than seeds with fruit pulp, a significant decrease in mean germination time for *M. lanssensianus* (Table 4). Funicular pulp produces allelopathic substances that inhibit seed germination in some cacti species and participation of animals that consume this pulp efficiently and remove this chemical barrier facilitate germination (Meiado et al. 2012). For example, seeds of *X. gounellei* that remained with

the funicular pulp had delayed germination and showed less germinability compared to seeds consumed by lizards (Gomes et al. 2016) and birds (Gomes et al. 2017). Germination of seeds in a shorter time is a strategy that favors the establishment of cacti seedlings in the field during the short period of water availability in the Caatinga's rainy season (Gomes et al. 2016). Despite removing funicular pulp and defecating intact seeds, the low number of seeds in *T. hispidus* scat precluded germination tests addressing the effects of seed passage through its digestive tract. Therefore, future studies should evaluate these effects on *M. lanssensianus* seeds and other cacti species with frugivory records by this lizard (*X. gounellei* and *Pilosocereus pachycladus* subsp. *pernambucoensis* (Ritter) Zappi) (Gomes et al. 2016; Sousa Neto et al. 2021).

Flowering was not detected in *M. lanssensianus* individuals and flowers were classified with complete cleistogamy (Culley and Klooster 2007). Cleistogamy is a type of autogamy in which unopened flowers are capable of autonomous self-pollination resulting in fruit and seed set (Wang et al. 2019). This reproductive strategy may be influenced by ecological factors, ensuring the reproductive success in stressful and unpredictable environments as well as in pollinator-scarce habitats (Culley and Klooster 2007; Wang et al. 2019). Cleistogamous flowers of *M. lanssensianus* ensure fruit production throughout the year. Cacti species are typically animal-dependent for pollination, self-incompatible, have bisexual flowers and inhabiting environments under extreme conditions (Mandujano et al. 2010; Schlumberger 2010; Guerrero et al. 2019). Among *Melocactus* spp., cross-pollination by hummingbirds is the common mode of pollination for their conspicuous tubular flowers and cleistogamy is rare (Taylor 1991; Taylor and Zappi 2004). Nevertheless, there are autogamic and self-compatible species in the genus [*M. curvispinus* (Nassar and Ramírez 2004); *M. paucispinus* (Colaço et al. 2006); *M. andinus* R. Gruber ex N.P. Taylor and *M. schatzlii* (Nassar et al. 2007); *M. intortus* (Mill.) Urb. (Fagua and Ackerman 2011); *M. ernestii* subsp. *ernestii* (Gomes et al. 2014b)]. In the cactus family, cleistogamic flowers have been reported also in *Frailea* spp. Britton & Rose (Rowley 1980; Schlindwein 1995; Carneiro et al. 2006).

The fruiting of *M. lanssensianus* is continuous (sensu Newstrom et al. 1994), peaking during both the

dry and rainy seasons. This continuous pattern has been observed in other species of *Melocactus* in arid and semiarid environments (Nassar and Ramírez 2004; Colaço et al. 2006; Casado and Soriano 2010; Fagua and Ackerman 2011; Gomes et al. 2014b). Guerrero et al. (2012) hypothesized that *Melocactus* species fruiting during most of the year could promote a close dependence by the lizards on Melocacti fruit as their main source of water. We recorded visits by *T. semitaeniatus* in all months of *M. lanssensianus* fruiting, while *T. hispidus* showed a seasonal pattern with visits only during dry months. Both lizard species showed more frugivory interactions in the dry season, with peak visits in dry months. *M. lanssensianus* fruits are composed mainly of water (85.3%), a valuable resource for lizards in this water-stressed ecosystem marked by a pronounced 8-month dry season.

Plant material, including leaves, flowers, and fruits has been reported as one of the three most important food items for *T. hispidus* populations in rocky outcrops areas in the Caatinga, especially during the dry season (Kolodiuk et al. 2010; Albuquerque et al. 2018). Seasonality of the Caatinga ecosystem may be a determining factor influencing lizards' foraging activities by cactus resources. Recent studies report on flower consumption of the cactus *Tacinga inamoena* (K.Schum.) N.P.Taylor & Stuppy (Paixão et al. 2021) and ingestion of pulp and seeds of the columnar cacti *X. gounellei* (Gomes et al. 2017) and *P. pachycladus* subsp. *pernambucoensis* (Sousa Neto et al. 2021) by *T. hispidus* during dry months in different Caatinga sites in northeastern Brazil. Likewise, fruit consumption among columnar species by *T. semitaeniatus* has been documented for *X. gounellei* (Gomes et al. 2016, 2017) and *Pilosocereus catiingicola* (Gürke) Byles & Rowley subsp. *salvadorensis* (Werderm.) Zappi (Silva et al. 2021b).

In a study carried out on rocky outcrops in the Caatinga, Gomes et al. (2014b) described *T. semitaeniatus* as a double mutualist of *M. ernestii* subsp. *ernestii*. In addition to the low arthropod supply in the environment and high local lizard densities (Cooper Jr and Vitt 2002; Olesen and Valido 2003), water scarcity of the environment is a condition that may lead to the consumption of fruits by lizards as sources of water and nutrients, increasing the probability of saurochory in the driest areas of the Caatinga (Gomes et al. 2014b). The authors suggest that this highly seasonal ecosystem, with an extreme dry season favors

the appearance of highly specialized interactions with strong dependence, as reported in the present study. Saurochory is a distinctive seed dispersal mode in the Caatinga, particularly in the Cactaceae (Leal et al. 2017). Caatinga biota includes over 21 species of *Melocactus* (Zappi and Taylor 2020) and nine species of *Tropidurus* (Mesquita et al. 2017). We suggest that other *Tropidurus-Melocactus* interactions remain to be described in the Caatinga.

Despite their ecological relevance, a third of the world's cactus species are at risk of extinction (Goetsch et al. 2015) and Cactaceae is the 6th most endangered family of the Brazilian flora (Martinelli et al. 2013). *M. lanssensianus* is categorized as endangered in both the IUCN Red List and the Brazilian Red List (Braun and Taylor 2013; Machado et al. 2013). In the study site, the main threats to this species are invasive grasses, mining, livestock animals (e.g., goats and cattle), intentional fires, motocross, and an annual religious celebration (Gomes et al. *in press*). The day celebration of Nossa Senhora da Assunção has been held on August 15th for about 100 years. On this date, mass and cultural celebration occurs, and thousands of people climb the granitic outcrops for devotion, traditionally setting fire on the vegetation during the conclusion of the celebration (Lima 2018). In the highest outcrop of the Pão de Açúcar Ranch, there were no reproductive individuals, solely seedlings and young plants, a clear consequence of anthropogenic impacts.

Given this context of a disturbed ecosystem associated with reduced population size and restricted distribution, it is clear that ex situ and in situ conservation support are urgent. Some initiatives have been conducted through educational actions and distribution of promotional materials to students and the local community, participation on a local radio program talking about the importance of conservation as well as in vitro propagation of 300 seedlings to establish an ecological restoration program to recover the population in their natural environment (Gomes et al. 2020). Further, we highlight the relevance of studies addressing reproductive biology aspects to assist conservation actions. The mutualistic interactions described here show that *M. lanssensianus* depends on lizards for an efficient seed dispersal service, such that lizards are essential to ensure reproductive success and survival of this endangered cactus species.

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Data availability The collected data are not deposited in any database.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest related to the publication of this manuscript.

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