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**Interações entre cactos e vertebrados na Caatinga, floresta tropical seca do
nordeste brasileiro**

Interactions between cacti and vertebrates at Caatinga, tropical dry forest in northeastern
Brazil

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VIRGÍNIA HELEN FIGUEIREDO PAIXÃO

**INTERAÇÕES ENTRE CACTOS E VERTEBRADOS NA CAATINGA,
FLORESTA TROPICAL SECA DO NORDESTE BRASILEIRO**

**INTERACTIONS BETWEEN CACTI AND VERTEBRATES AT CAATINGA,
TROPICAL DRY FOREST IN NORTHEASTERN BRAZIL**

Dissertação apresentada ao programa de Pós-Graduação em Ecologia da Universidade Federal do Rio Grande do Norte, como parte das exigências para a obtenção do título de Mestre em Ecologia

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Dra. VANESSA GRAZIELLE NÓBREGA GOMES, INSA

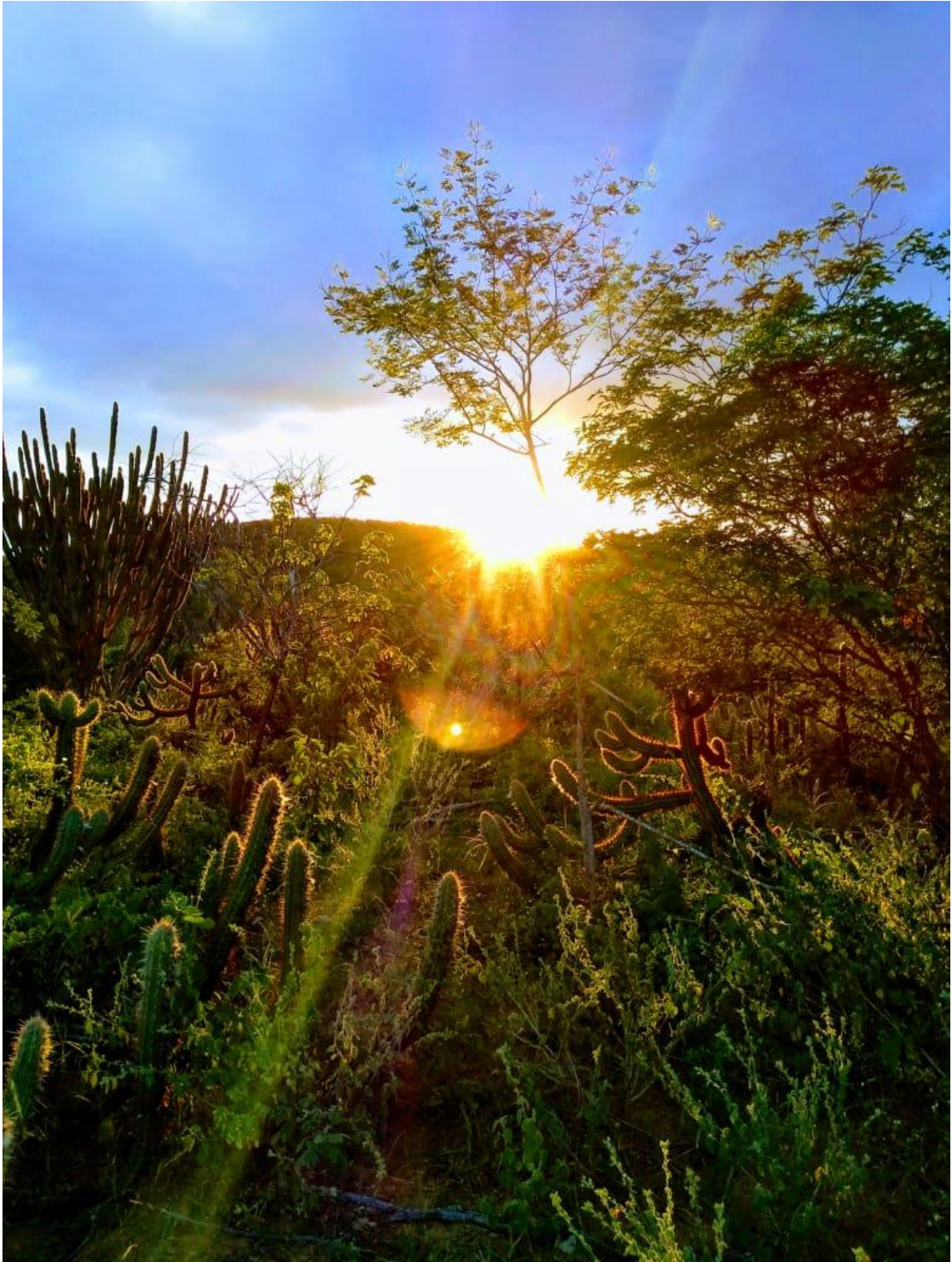
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Presidente



*É que o sertão é mais que uma região fisiográfica.
Além da terra, das plantas, dos bichos e do bicho-homem – tem o seu viver, os seus
cheiros, cores e ruídos.*

Oswaldo Lamartine

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Abstract: Cacti species play a major role in frugivory networks in arid and semiarid ecosystems. Several studies reinforced the role of birds, bats, and lizards as effective cacti seed dispersers, although little is known about how these interactions are distributed in a network. Our objective was to describe network structure (nestedness and modularity) of mutualistic network of cacti-seed dispersal by vertebrates at Caatinga, Rio Grande do Norte State, Brazil. We also seek to identify how much cacti species differ on the community of frugivores that feed on their fruits using the Bray-Curtis dissimilarity index. For that, we monitored frugivory in six cacti species (globular *Melocactus zehntneri*, prickly-pear *Tacinga inamoena*, columnar *Pilosocereus gounellei*, *P. chrysostele*, *P. pachycladus*, and *Cereus jamacaru*) using camera-traps during eleven months, contemplating both daytime and nighttime. We found 23 vertebrate species feeding on four cacti species fruits, except on *T. inamoena* and *P. chrysostele*, and these interactions were not nested or modular, meaning that interactions within network are relatively symmetric. Our data show that cacti have a generalist strategy of attracting a wide variety of animals that provide different dispersal services, such as birds, reptiles, and mammals, all of which were recorded as primary dispersers. Despite this generalization, columnar cacti *P. pachycladus* and *C. jamacaru*, shared a similar community of frugivores, mainly birds. The columnar cactus *P. gounellei* was more similar to the globular *M. zehntneri*, and both had fruits consumed mainly by lizards (*Tropidurus hispidus*) and mammals, probably because they provide fruits closer to the ground. During our study, we found new interactions between lizards *Salvator merianae* to *P. gounellei* fruits and *Tropidurus hispidus* feeding on *T. inamoena* flowers, recorded during the eleven months survey with camera-traps. *S. merianae* consumed *P. gounellei* fruits in two different days, while *T. hispidus* were recorded eating four *T. inamoena* flowers in four different days in three months. Cacti offered fruits continuously throughout the year, maintaining different groups of animals that potentially play a complementary role in the dispersion of cactus seeds and, therefore, these mutualistic interactions must be considered in the conservation and restoration of semiarid environments such as Caatinga.

Key-words: Plant-animal interactions; Frugivory; Cactaceae; Caatinga; Seed dispersal; Florivory; Nestedness; Modularity.

Resumo: Interações mutualísticas entre plantas e animais dispersores de sementes são cruciais para a manutenção da biodiversidade. O papel de aves, morcegos e lagartos enquanto dispersores de sementes de cactos já foram elucidados, mas ainda se sabe pouco sobre como essas interações estão distribuídas dentro de uma rede de interação. O objetivo dessa dissertação foi descrever a estrutura (aninhamento e modularidade) da rede dispersão de sementes de cactos por vertebrados na Caatinga do Rio Grande do Norte, Brasil. Para isso, nós monitoramos ao longo de onze meses a frugivoria de seis espécies de cactos (globular *Melocactus zehntneri*, prickly-pear *Tacinga inamoena*, colunares *Pilosocereus gounellei*, *P. chrysostele*, *P. pachycladus* e *Cereus jamacaru*) com armadilhas fotográficas, contemplando tanto o período diurno quanto noturno. Também buscamos identificar o quanto as espécies de cactos diferem em relação à comunidade de frugívoros que se alimentam de seus frutos utilizando o índice de dissimilaridade de Bray-Curtis. Nós encontramos 23 espécies de animais vertebrados interagindo com quatro espécies de cactos, exceto em *T. inamoena* e *P. chrysostele*. A rede de interação não apresentou padrão aninhado nem modular, indicando que as interações entre cactos e vertebrados são relativamente simétricas dentro da rede. Os resultados sugerem que os cactos possuem uma estratégia generalista, atraindo diversos animais que podem contribuir diferentemente na dispersão de sementes, incluindo aves, répteis e mamíferos, todos esses aqui identificados atuando como dispersor primário. Apesar dessa generalização, nós observamos que os cactos colunares mais altos, *P. pachycladus* e *C. jamacaru*, compartilharam uma comunidade semelhante de frugívoros, principalmente aves. Já o cacto colunar *P. gounellei* foi mais semelhante ao globular *M. zehntneri*, e ambos tiveram frutos consumidos principalmente por lagartos (*Tropidurus hispidus*) e mamíferos, provavelmente por disponibilizarem frutos mais próximos do chão. Identificamos novas relações de frugivoria entre *P. gounellei* e o lagarto *Salvator merianae* e de florivoria entre *T. inamoena* e o lagarto *T. hispidus*, durante os onze meses de monitoramento de cactos com armadilhas fotográficas. *S. merianae* consumiu frutos de *P. gounellei* em dois dias diferentes, enquanto *T. hispidus* foi registrado consumindo quatro flores de *T. inamoena* em quatro dias diferentes em três meses. Os cactos ofereceram frutos continuamente ao longo do ano mantendo diferentes grupos de animais que potencialmente desempenham um papel complementar na dispersão de sementes de cactos e, portanto, essas interações mutualísticas devem ser consideradas na conservação e restauração de ambientes semiáridos como a Caatinga.

Palavras-chave: Interações planta-animal; Frugivoria; Cactaceae; Caatinga; Dispersão de sementes; Florivoria; Aninhamento; Modularidade.

GENERAL INTRODUCTION

Seasonally dry tropical forests (SDTF) occur in regions characterized by rainfall shorter than 1.800 mm/year and a marked dry season when rainfall is less than 100 mm/month (Pennington et al. 2009). SDTFs are composed mostly by deciduous vegetation during the dry season, generally smaller in stature than wet tropical forest and mainly composed by thorny and succulent species (Murphy and Lugo 1986, Pennington et al. 2009). SDTFs have been neglected in studies in comparison with tropical rain forest, which is one of the reasons why these regions are thought to be less complex in ecological interactions (Sánchez-Azofeifa et al. 2014). It is also subjected to intense deforestation, land use, and human expansion (Sánchez-Azofeifa et al. 2014).

In Northeast Brazil, the Caatinga is a well-recognized ecological region located in the semiarid in which the dominant vegetation type is SDTF (Silva et al. 2017). Similarly with the others dry forests, basic ecological synthesis about ecological interactions in the Caatinga is still lacking (Leal et al. 2017). Studies have emphasized that the loss of ecological interactions can affect network stability (Bastolla et al. 2007, Bastazini et al. 2018). As well as in other SDTFs in the tropical region, Caatinga ecosystem has been subjected to main disturbances arising from human activities such as fuelwood extraction, livestock farming, and poaching (Ribeiro et al. 2015, Marinho et al. 2016). In a changing world, mutualistic interactions of seed dispersal are especially vulnerable to anthropogenic disturbances (Neuschulz et al. 2016). Therefore, it is necessary to identify and understand mutualistic interactions of seed dispersal in the Caatinga before it is lost or disrupted.

Cactaceae is an endemic botanical family of the Americas, with more than 1,300 species in North, Central and South America and Caribbean (Nobel 2002, Ortega-Baes

and Godínes-Alvarez 2006, Zappi et al. 2018). Due to their resistance to semiarid climates, cacti species can handle to be abundant in this harsh condition (Anderson 2001, Bravo-Hollis 1978). In the Caatinga, Cactaceae family have 22 genera and 73 species, being one of the five species rich families in Sedimentary Caatinga (Queiroz et al. 2017). They are present in its various morphologies such as columnar and globular, where they often dominate the landscape (Nobel 2002, Bustamante and Búrquez 2005, Zappi and Taylor 2004). On arid environments the anthropogenic pressure is very high, threatening mostly the Cactaceae (cacti) family – 31 % of 1,478 species are threatened with extinction (Goettsch et al. 2015). At the Caatinga, 32 cacti species are threatened, including *Pilosocereus chrysostele* (NT, IUCN) being one of the ten botanic families more threatened in Brazilian territory (Machado et al. 2013). The main threats this family faces are the conversion of forests for agricultural and aquaculture use, collection of live plants and seeds as biological resources and commercial use, and livestock ranching (Goettsch et al. 2015).

Many animal species, including humans, rely on cacti resources for food (Chaves and Barros 2015). Their fleshy fruits sustain a wide variety of animals, and the role of birds and lizards as seed dispersers of columnar and globular cacti, respectively, is already known (Nobel 2002, Gomes et al. 2014, 2016). How interactions among cacti and vertebrate species are structured within a network is still to be discovered. In this dissertation we aimed to study the network of frugivory interactions of Cactaceae species with vertebrates in the Caatinga. This document is composed by two chapters focussing on the ecological interactions between cacti and vertebrates.

In the first chapter “Network structure and frugivory patterns of Cactaceae in Caatinga, a Brazilian dry forest” we aimed to explore network patterns of the cacti-

frugivore network by vertebrates, as well as to discuss the role of animals as potential cacti-seed dispersers.

In the second chapter “Interactions between lizards and cacti in the Caatinga” we explore new discoveries about ecological interactions between cacti and lizards, such as the first record of florivory of *Tacinga inamoena* by *Tropidurus hispidus* and the first record of frugivory of *Pilosocereus gounellei* by *Salvator merianae*. This chapter is composed by two *short communications*.

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**Chapter I - Network structure and frugivory patterns of Cactaceae in Caatinga, a
Brazilian dry forest**



Introduction

Plant-animal mutualistic interactions of seed dispersal have a key role in the maintenance of biodiversity (Bascompte and Jordano 2007, Andresen et al. 2018). The vast majority of seeds in the tropics are imbedded in a fleshy pulp of different shape and colours, adapted to endozoochory (seed dispersal by animals) (Estrada and Fleming 1986, Jordano 2000). When the animals feed upon the fruits, they swallow intact seeds and release them in a vacant site, thus promoting the regeneration of ecosystems (Howe and Smallwood 1982, Schleuning et al. 2015). In fact, many tree species in tropical rainy forest (50-90%) and tropical dry forest (30%-35%) rely on birds and mammals to disperse their seeds (Howe and Smallwood 1982, Griz and Machado 2001, Lopezaraiza-Mikel et al. 2014). Those animals, in turn, rely on fruits for a living, in a way that this mutualism shapes the evolutionary relationship of such species (Herrera 1985, Fleming and Kress 2013). Unfortunately, seed dispersal services are one of the biological interactions most vulnerable to anthropogenic disturbance in tropical forests (Neuschulz et al. 2016).

Interacting species form a complex network of interactions with structural properties that can be accessed through network graph analyses (Bascompte and Jordano 2006, 2007). Mutualistic interactions can be arranged in a matrix where animals can be set in the columns, plants in the rows, and cells are filled with qualitative (0/1) or a quantitative measure of interaction (i.e., relative frequency of visits) (Jordano 1987, Bascompte and Jordano 2006). Network tools have proved useful to quantify interactions between mutualists in entire communities, to help understand the structure of network interactions, addressing which animals eat fruits and potentially disperse seeds (Howe 2016). Insights gained from network analyses showed that interactions in mutualistic networks (e.g. plant-pollinator, seed-dispersal) tend to be nested (Bascompte

et al. 2003, Dupont et al. 2003, Almeida-Neto et al. 2007, Dugger et al. 2018). Nested networks are formed by a small core of generalist plant and animal species interacting with each other, and this core holds a large fraction of the total number of interactions (Bascompte et al. 2003). In a nested pattern, specialist tends to be rare and interact with generalists, which tend to be more ubiquitous, since they rely on multiple resources (Bascompte et al. 2003). Besides providing a pathway for rare species to persist, nestedness is also thought to increase biodiversity and robustness against local extinctions (Bascompte and Jordano 2006, Bastolla et al. 2007, Tylianakis et al. 2010, Bastazini et al. 2018).

A recurrent structure of many types of networks is being organized into modules, which means the existence of sub-communities within network (Olesen et al. 2007, Dáttillo et al. 2016). A modular pattern imply species interacting strongly within a compartment and few weak interactions between them (Bascompte and Jordano 2006). Network modules usually reflect a match between fruits characteristics and the animals that eat them (Dehling et al. 2015, Muñoz et al. 2016). Differences in accessibility of consumable rewards, such as fleshy fruits, may impose limitations to frugivore assemblages (Vázquez et al. 2009). Plant height is usually related to fruit accessibility and can affect the feeding behaviour of frugivores that have a preference or are limited to certain forest strata (Gondim 2001, Schleuning et al. 2011, Dehling et al. 2014). Seed dispersal services, in turn, depend strongly on the variety of animal taxa, such as birds, bats, primates, rodents, lizards, and fishes, thus generating different modules (Donatti et al. 2011). Different species traits imply that species have different ecological requirements and thus affect the ecosystems in different ways – they can be similar or “redundant” in their traits (Bastazini et al. 2018). Because modules can be complementary or redundant with each other, it is essential to comprehend the existence

of a mosaic of modules and how seed dispersal services are generated (Mello et al. 2011).

Cacti species play a major role in frugivory networks in arid and semiarid ecosystems (Bravo-Hollis 1978, Rojas-Aréchiga and Vázquez-Yanes 2000). In such environments, where water and food resources are in short supply most part of the year, cacti stand out for their fruit rich in water and sugar, and its mucilaginous pulp (Quirino 2006, Vázquez-Castillo et al. 2019). Most cacti species produces fleshy fruits with bright colours (e.g., the purple pulp of *Pilosocereus* spp.), attractive to animals (Bregman 1988). In general, cacti fruits contain many small seeds characterized by a thick or resistant testa which can bear stomach acids and enzymes, such as in *Opuntia* and *Melocactus* species, proper to be dispersed by animals (Bregman 1988, Rojas-Aréchiga and Vázquez-Yanes 2000). Therefore, cacti potentially attract a huge variety of vertebrate frugivores that can act as seed dispersers, such as birds, bats, reptiles, and primates (Figueira et al. 1994, Soriano et al. 1999, Soriano and Ruíz 2002, Taylor and Zappi 2004, Abreu et al. 2016). In fact, zoochory is the commonest mode of seed transportation for cacti seeds, with animals being responsible for the transport of seeds to safe sites and for the increase in seed germination after the gut passage (Nobel 2002, Figueira et al. 1994, Soriano et al. 1999). Also, in *Pilosocereus* spp. fruits, animals remove secondary compounds that reduce seed germinability, present in their funicular pulp (Meiado et al. 2012). Consequently, fruit consumption by animals is a fundamental step for cacti seed dispersal, promoting the resilience and regeneration of cacti communities (Howe and Smallwood 1982, Baños-Villalba et al. 2017).

In this study, we are interested in a Brazilian seasonally dry tropical forest (Caatinga) where cacti from different morphologies (globular, flattened-cladode, columnar) are dominant from forest understory to canopy. Previous studies of frugivory

in Cactaceae focused on a particular cactus species or specific groups of animals (e.g. birds, bats) (Soriano et al. 1999, Figueira et al. 1994, Gomes et al. 2014, 2016, 2017, Santos et al. 2019). Here we aimed to build and investigate the structure of the first cacti-frugivore network with all its potential dispersers with an unprecedented approach for the Cactaceae family, with equal sampling effort for daytime and nighttime. We believe that modularity in our network would be a consequence of the constraints imposed by different cacti height to animal with different mobility. In this way, we expected to find different modules, one composed by less mobile animals, such as non-flying mammals and reptiles with the lowest cactus (*M. zehntneri* and *T. inamoena*), while the tallest cacti species (*P. gounellei*, *P. pachycladus*, and *C. jamacaru*) will form modules with birds, bats and/or arboreal mammals. We also aimed to describe patterns of cacti frugivory, addressing: what animal species are frugivores of six cacti species? Is there difference in animal classes that feeds on cacti species from different plant height? We expect that this study help us uncover the ecological process involving cacti frugivory in a semiarid landscape where cacti and animals rely on each other.

Material and methods

Study site

Our study was conducted at Lajes municipality, in a private property named Fazenda Santo Antônio, located in the central portion of Rio Grande do Norte State (05°47'55.5"S 36°14'22.2"W), Northeastern Brazil (Fig 1). Regional climate is dry semiarid with a marked and extended dry season (rainfall < 50 mm/month) from August to December. Rainfall is erratic, unpredictable and usually occurs from February to May, when the total amount of precipitation reaches 350 mm (Szilagyi 2007, Brito et al. 2017, Tomasella et al. 2018, Supplementary material I). The area is characterized by a

cacti scrub physiognomy, with columnar cacti species mainly from *Pilosocereus*, *Cereus*, *Tacinga*, and *Melocactus* genera dominating the landscape (Fig. 2). Lajes houses the largest continuous fragment of Caatinga ($\cong 50,000$ ha) vegetation of the state and has been considered one of the priority areas for biodiversity conservation of the Caatinga biome due to the presence of a representative fauna (Venticinque et al. 2015, MMA Portaria nº 463, 2018). This dry forest have a discontinuous canopy (2-5 m in height) represented by woody plants, such as Fabaceae, Euphorbiaceae, with abundant Cactaceae and Bromeliaceae. The study site is covered with patches of mature forest and secondary forest with at least 30 years of regeneration. In the past, the area was used for marble extraction. Nowadays, the area is subjected to continuous human disturbance as livestock, hunting and more recently installation of wind farms.

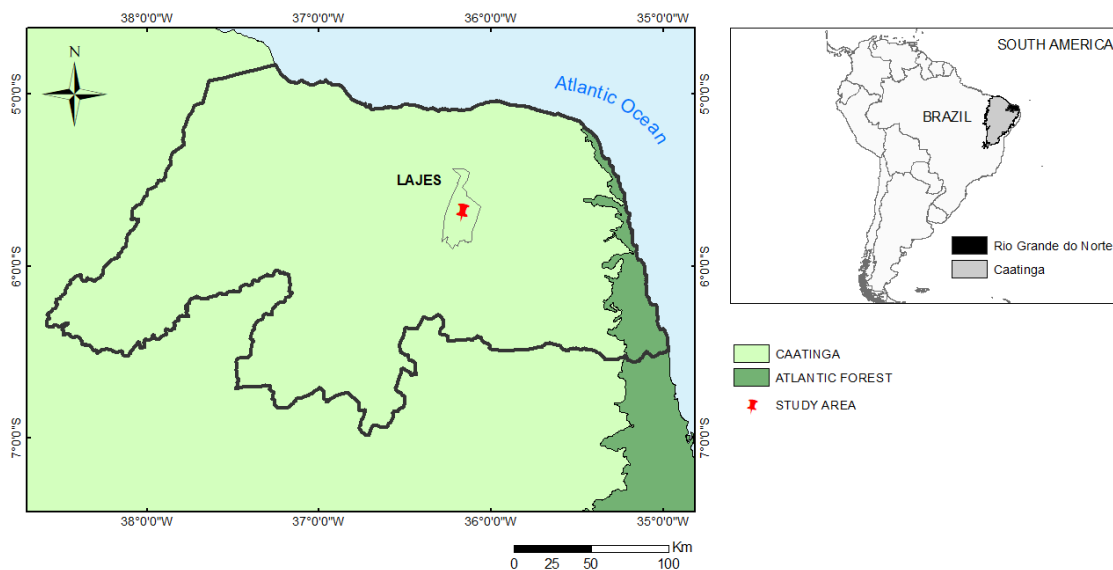


Figure 1. Study site where we collected data about cacti-frugivore interactions with vertebrates at a Caatinga site in Lajes municipality (05°47'55.5"S 36°14'22.2"W), Rio Grande do Norte State, northeastern Brazil. Source: Fernanda Lamin, 2020.



Figure 2. Study site at Lajes municipality, Rio Grande do Norte State, Brazil

Study species

We have studied all six Cactaceae species known to occur in Santo Antônio private farm, Lajes, RN: *Melocactus zehntneri* (Britton & Rose) Luetzelb. (Fig. 3A), *Tacinga inamoena* (K.Schum.) N.P.Taylor & Stuppy subsp. *inamoena* hereafter *T. inamoena* (Fig. 3B), *Pilosocereus gounellei* (F.A.C.Weber) Byles & Rowley subsp. *gounellei* hereafter *P. gounellei* (Fig. 3C), *P. chrysostele* (Vaupel) Byles & G.D.Rowley subsp. *chrysostele* hereafter *P. chrysostele* (Fig. 3D), *P. pachycladus* F.Ritter subsp. *pachycladus* hereafter *P. pachycladus* (Fig. 3E), and *Cereus jamacaru* DC. subsp. *jamacaru* hereafter *C. jamacaru* (Fig. 3F). They are all endemic to Brazil, and are among the most widespread Cactaceae species in national territory, growing in a wide variety of soils types, with almost no habitat restriction (Menezes et al. 2011, 2013, Zappi et al. 2018). Their fruits of different sizes, shapes, bright colours (orange-reddish-

purple; Fig. 3, Tab. 1) and small seeds (1-3 mm) offers a fleshy pulp rich in water content which are consumed by a wide range of generalist frugivores that swallow part of the pulp and may be capable to disperse their seeds due to its small size (Supplementary material II, Do Nascimento et al. 2011, and see references in Table 1).



Figure 3. Fruits of the six cacti species present at a Caatinga site in Lajes municipality, Rio Grande do Norte State, northeastern Brazil. A) *Melocactus zehntneri*. B) *Tacinga inamoena*. C) *Pilosocereus gounellei*. D) *Pilosocereus chrysostele*. E) *Pilosocereus pachycladus*. F) *Cereus jamacaru*.

Table 1. Biological information about the six cacti species known to occur at the study area at a Caatinga site in Lajes municipality, Rio Grande do Norte State, northeastern Brazil. Cactus height (m), Spines (length in mm), fruit size (length x diameter cm), seed size (length x diameter mm) and seeds (N) refers to mean values according to literature, which are indicated by the numbers following the species name.

Cactus	Habit	Morphology	Height	Spines	Fruit Size	Pericarp color	Pulp color	Fruit Type	Seed size	Seeds	Dispersers
<i>Melocactus zehntneri</i> ^{2,3,4,5}	Globose	Globular	≤ 0.4	20-30	≤ 2 x 1	Lilac	Translucent	Conical	≤ 1 x 1	20-45	Lizards
<i>Tacinga inamoena</i> ^{1,2,3,4}	Subshrub	Flattened-cladode	≤ 1	Glochids	≤ 3	Orange	Translucent	Globose	≤ 3	Dozens	Mammals?
<i>Pilosocereus gounellei</i> ^{2,3,4,6,7,8,9}	Shrub	Columnar	≤ 3	10-150	≤ 4 x 6	Pinkish	Magenta	Globose	≤ 1 x 1	≤ 4000	Birds, Mammals, Lizards, Ants
<i>Pilosocereus chrysostele</i> ^{2,3,4,8,9}	Tree	Columnar	≤ 6	2-28	≤ 2 x 2	Magenta	Magenta	Globose	≤ 1 x 1	Dozens	Birds, Ants
<i>Pilosocereus pachycladus</i> ^{2,3,4,7,9,10}	Tree	Columnar	≤ 10	1.5-30	≤ 4 x 5	Purplish	Magenta	Globose	≤ 2 x 1	Hundreds	Birds, Primates
<i>Cereus jamacaru</i> ^{2,3,4,7,11,12,13}	Tree	Columnar	≤ 6	7-150	≤ 10 x 8	Red	White	Ellipsoid	≤ 3 x 2	Hundreds	Birds, Primates

¹ Lambert 2009, ² Forzza et al. 2010, ³ Menezes et al. 2011, ⁴ Menezes et al. 2013, ⁵ Taylor 1991, ⁶ Abud et al. 2012, ⁷ Abreu et al. 2016, ⁸ Gomes et al. 2017, ⁹ Zappi 2000, ¹⁰ Abud et al. 2010, ¹¹ Abud et al. 2013, ¹² Gomes et al. 2014, ¹³ Amora et al. 2013.

Fruiting phenology

We collected monthly information about fruit availability at the cacti community in order to understand better which cactus could be interacting with animals every month, from September 2018 to July 2019, with a gap in June, due to logistical issues, totalling ten months. For collecting phenological data, we have established five plots in the study area based on pre-existing trails, covering a total area of 5,250 m². All plots had 5 m width but different extensions (130 m, 120 m, 100 m, 300 m, and 400 m), because trails length were different. We then quantified and summarized the number of cactus individuals per species, in any size class, present in the plots (Tab. 3). In the case of the *T. inamoena*, we considered one individual the whole agglomeration. Every month, we quantified the number of reproductive individuals of the six cacti species monitored with unripe or ripe fruits, regardless the quantity. We then calculated the monthly percentage of fruiting individuals for every cactus species dividing the number of individuals with fruits (sum of all plots) by the total individuals cactus (sum of the individuals number at all plots). Phenological information monitoring would prevent the lack of frugivory interactions to a given cactus through phenological mismatches.

Frugivory records

We monitored vertebrate frugivory events to the six cacti species studied here throughout 11 months, from September 2018 to July 2019, with cameras trap (Bushnell 8 MP Trophy Cam). We searched for cactus individuals of every species with ripe fruits over the study area, and the individuals chosen to be monitored with cameras were not restricted to those observed in the phenology. We tried to keep the sample effort of camera-days balanced between the cacti species by monitoring an equivalent number of individuals of every species in every month (Tab. 2). In despite of it, there were natural events we could not control, and that influenced sample effort. These

events were batteries or memory card issues, mainly due to overheating, and the lack of fruits that could be properly monitored.

We installed the cameras over the study area, tied in trees or in wooden stakes when necessary to reach the fruits of tall columnar cacti (> 4 m height), and keeping a distance of at least 70 m between cactus of the same species monitored at the same time. We prioritized individuals with more ripe fruits at the occasion. We set the cameras close (2–5 m) and toward a cactus fruit ensuring that all fruits available were framed by the camera. We programmed them to take two pictures followed by a 10 seconds video, in minimal intervals of one minute when triggered. This setting was appropriate to detect fruit consumers and the videos helped ensure fruit consummation; this time interval aimed to prevent that the cameras took many redundant registers. We then left the cameras in the field working 24 h per day to maintain a similar daytime and nighttime sample effort and to detect elusive, scarce or nocturnal potential seed dispersers (Blanco et al. 2019). After a period of 30 to 50 days, we removed the cameras to collect their memory cards and to install them in other cacti, because usually this time was enough for the fruit whether to be ripen and fall or to be entirely consumed. We were unable to properly monitor the cactus species *Pilosocereus chrysostele* due to field constraints such as cameras not working for a month, and memory card and batteries overheating. Because of that, we excluded *P. chrysostele* from the graph and network analyses due to its unbalanced sample effort.

At the laboratory, we analysed all the content registered in the cameras to quantify the fruit consumption events. We considered one event of seed dispersal when: there was a photo/video of an animal eating one or more fruits; when there was a photo/video of an animal standing in front of the fruit and in the next photo/video, if less than five minutes after the previous, the animal and the fruit were gone; when there was a

sequence of photos/videos of the animal eating the fruit continuously without leaving. We considered two or more events of frugivory when: an animal was seen in a photo/video eating and then leaving the fruit and in the next photo/video coming back and eating again; two individuals eating the same or different fruits in the same photo/video. For each seed dispersal event we recorded: the cactus species, animal species, date, time of the day and fruit height. We estimated the fruit height visually in the field when installing the cameras for all cacti species except *M. zehntneri*, for which we used the mean individual height established in the literature (Menezes et al. 2013). We identified every animal at species level when possible using field guides and checking with specialists (Emmons and Feer 1997, Bovincino et al. 2008, Freitas 2012, Sigrist 2014, Freitas 2015). To assess whether our records represented well the vertebrate community that utilizes cacti fruits, we performed species accumulation curves for every cacti species in software EstimateS 9 (Colwell, 2013).

Table 2. Sample effort of camera days and number of individuals monitored in each month in parenthesis for each cactus species at a Caatinga site in Lajes municipality, Rio Grande do Norte State, northeastern Brazil. Monthly average of camera-days is the total of camera-days divided by the number of months a given cactus species was monitored. “–” refers to months that the given species was not monitored due to the lack of fruits available. The monthly average of individuals monitored in parenthesis refers to the number of individuals monitored each month with pseudoreplication, which means that the same cactus individual could have been monitored for more than one month (e.g. started being monitored in 15th January until 15th February, thus being computed as one individual in each month).

Species	Effort in camera-days (N plants monitored)											Monthly average	Total
	Sep/2018	Oct/2018	Nov/2018	Dec/2018	Jan/2019	Feb/2019	Mar/2019	Apr/2019	May/2019	Jun/2019	Jul/2019		
<i>Melocactus zehntneri</i>	10(01)	13(01)	48(03)	27(03)	3(02)	69(05)	80(07)	77(03)	129(08)	204(07)	51(06)	64.64(4.18)	711 (18)
<i>Tacinga inamoena</i>	12(02)	31(02)	52(03)	46(04)	59(03)	48(03)	67(05)	41(03)	49(03)	45(02)	-	45(3)	450 (11)
<i>Pilosocereus gounellei</i>	12(01)	13(01)	44(02)	57(04)	31(02)	36(03)	5(02)	-	141(10)	222(09)	60(07)	62.1(4.1)	621 (17)
<i>Pilosocereus chrysostele*</i>	-	-	32(04)	5(01)	4(03)	44(03)	2(01)	-	-	-	-	17.4(2.4)	87 (8)
<i>Pilosocereus pachycladus</i>	10(01)	31(02)	76(05)	33(02)	02(01)	28(01)	46(04)	100(04)	84(08)	30(01)	08(01)	40.73(2.73)	448 (16)
<i>Cereus jamacaru</i>	-	-	-	-	08(05)	132(06)	130(08)	75(03)	136(12)	180(09)	38(09)	99.85 (7.43)	699 (18)

* Excluded from the analysis due to unbalanced sample effort.

Network structure

We calculated nestedness and modularity, two of the most commonly used network-level indices that describe the organization of species interactions within the entire network (Bascompte et al. 2003, Olesen et al. 2007). For that, we built a quantitative interaction frequency matrix where the cacti species were set in the lines (*lower* level) and the vertebrate species were set in the columns (*higher* level). Cells were filled with an interaction frequency that we defined here as the number of seed dispersal events by vertebrate frugivores on a cactus species divided by the sample effort (camera-days) times 100. Animal species strength in a network (often measured by means of interaction frequencies) is positively related to the dependence of frugivore species on fruits (Fricke et al. 2017). We are aware that the animals dependence on plants do not always reflect effectively seed dispersal by animals (Howe 2016). However, focussing on fruit-removal stage is a suitable proxy of actual seed dispersal success (Simmons et al. 2018). We built a network graph using the quantitative interaction frequency matrix which was also used to perform network metrics analyses. Network graph was obtained with the function *plotweb* of the R-package “bipartite” (Dormann et al. 2008).

Once metrics for calculating the degree of nestedness in weighted networks can be strongly affected by weak links, we chose to use NODF metrics for binary networks. For that, we transformed our weighted data into binary data (presence / absence of interaction), and calculated the degree of nestedness in the network using the metric NODF (Almeida-Neto et al. 2007). The NODF metric is unrelated to matrix shape and size, and values of nestedness ranges from 0 (not nested) to 1 (perfectly nested) (Almeida-Neto et al. 2007). The significance of this metric was estimated with r1 model

in vegan R-package, a non-sequential algorithm for binary matrices that preserves the site (row) frequencies, but uses column marginal frequencies as probabilities of selecting specie (Oksanen et al. 2019). NODF observed was considered significant if greater than 95% of randomized values (p value = 0.05).

We analysed the modularity of the network with the QuanBiMo algorithm specifically designed for weighted bipartite networks, described in detail in Dormann and Strauss 2014. In this case, Modularity is measured by Q , which varies from 0 (no modules) to 1 (maximum degree of modularity). Modularity was calculated in software R with the package bipartite and the function computeModules and the function plotModuleWeb to visualize the matrix with modules. To test the significance of Q value, we randomized 1000 interaction matrices with the null model proposed by Vázquez et al. (2007), which preserves marginal totals (takes account of interaction abundance) and it keeps network connectance constant (Vázquez et al. 2007, Dormann et al. 2008). We then used the same Modularity algorithm described above to obtain estimates of Q for the null models. Null models were generated with the function *vaznull* with the R-package bipartite (Vázquez et al. 2007, Dormann et al. 2008).

Patterns of frugivory

We used Bray-Curtis (B-C) index to access how different are cacti species in terms of interacting animal species and number of interactions, using the interaction frequency matrix. Values of B-C index range from 0 to 1, where lower values indicate that cacti species interacts with a different set of animals. We expect that cacti that have similar height will share higher values of B-C, which means they share a similar set of interacting species. Analyses were performed on software PAST version 3.0.

We used the height each fruit was consumed to build a boxplot to explore whether there was difference in the mean height of fruits consumed by vertebrate classes (birds,

mammals, reptiles). We then calculated if the mean height per vertebrate classes were different using a Kruskal-Wallis test, once the ANOVA assumptions were not met by our data. Test was performed on software R (R Development Core Team, 2012).

Results

Fruiting phenology

Five out of six cacti species fruited continuously along the study period, which corresponded to both dry and rainy season (Tab. 3). The exception was the columnar *Cereus jamacaru* that only started fruiting with the beginning of the rainy season (Tab. 3, Supplementary material I). Fruiting occurred throughout the year mostly in low intensity. High frequency occurred between January and February when 20 to 67% of the individuals were fruiting.

Table 3. Monthly percentage (%) of the number of fruiting individuals per cactus species from September 2018 to July 2019 with a gap in June 2019 at a Caatinga site in Lajes municipality, Rio Grande do Norte State, northeastern Brazil. N is the sum of cactus individuals per species observed in the phenology each month, present in the plots. The wet and dry season months are indicated. The shading scale represents the intensity of the number of fruiting individuals from white (no fruiting individuals) to black (high frequency of fruiting cactus).

Species	Dry					Wet					
	N	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jul
<i>Melocactus zehntneri</i>	80	3	6	6	4	9	9	13	10	36	3
<i>Tacinga inamoena</i>	197	9	22	16	17	20	11	11	7	8	4
<i>Pilosocereus gounellei</i>	277	5	1	11	13	60	57	7	3	5	5
<i>Pilosocereus chrysostele</i> *	14		14	7	14	14	29		7	7	
<i>Pilosocereus pachycladus</i>	258	9	7	5	5	55	67	13	10	11	17
<i>Cereus jamacaru</i>	28					18	25	4	7	11	

* Excluded from further analysis.

Frugivory records and network structure

In a total of 2,929 camera-days of monitoring, we recorded 203 frugivory interactions, all of which vertebrates consumed the fruits directly from the plant (primary seed dispersal). The cumulative curves suggest that we were able to detect vertebrate species richness that utilizes cacti fruits (Fig. 4). The studied cacti species had frugivory interactions with 23 vertebrate species, including birds ($S = 13$ species), mammals ($S = 6$), and reptiles ($S = 4$). Of the recorded interactions with fruit consumption, 123 were made by birds, 58 by reptiles, and 22 by mammals (Tab. 4). We had birds, mammals and reptiles interacting with all the cacti species that had interactions, with exception from *P. pachycladus* that did not interact with reptiles. Birds consumed more frequently the columnar cacti, while reptiles were the main consumers of the globular cactus species *M. zehntneri* and the columnar *P. gounellei* (Fig. 5). No vertebrate species were seen eating *Tacinga inamoena* fruits but, interestingly, we recorded *T. hispidus* lizards eating their flowers (see chapter 2) while there were also fruits available.

The most frequent families recorded consuming cacti fruits were Tropicuridae (55 frugivory events), Psittacidae (33), Turdidae and Icteridae (23, both) (Tab. 4). The species that made a larger number of fruit consumption were the lizard *Tropidurus hispidus* (49), and the Cactus Parakeet *Eupsittula cactorum* (33) (Tab.4, Fig. 6). Those species fed on almost all studied cacti species, considering that *T. hispidus* only did not consume *P. pachycladus* fruits, and parakeets ate exclusively fruits from the columnar cacti species (*P. gounellei*, *P. pachycladus*, and *C. jamacaru*) (Tab. 4, Fig. 6). From the perspective of the cacti species, the columnar held most and an equivalent number of frugivory interactions (ca. $N = 60$) and species (ca. $N = 11$), being those mainly birds, with exception of the columnar *P. gounellei*, which was more consumed by lizards. In

relation to the short globular cactus *M. zehntneri*, it had a lower number of interactions and species in comparison to the columnar, and this consumption were made mainly by the *T. hispidus* lizard (Fig. 6).

The cacti-seed dispersal network was more nested than modular, although none of the metrics were significantly different than values derived from null models ($Q_{\text{obs}} = 0.39$, $Q_{\text{null}} = 0.41$; p value = 0.34; NODF = 41.73, p value = 0.06).

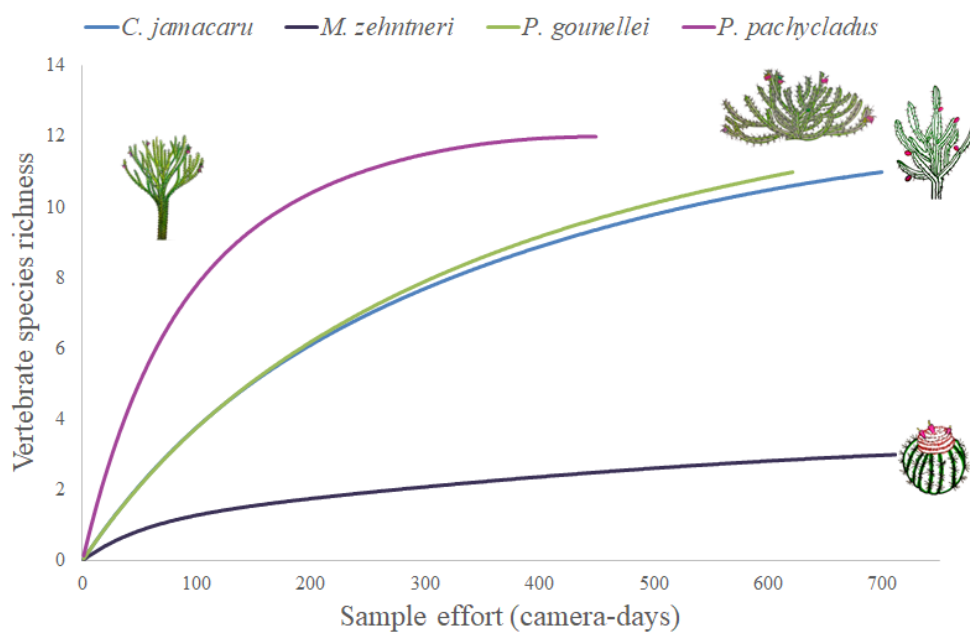


Figure 4. Cumulative curves of vertebrate species richness that consume cacti fruits at a Caatinga site in Lajes municipality, Rio Grande do Norte State, northeastern Brazil, from September 2018 to July 2019.

Table 4. Number of vertebrate species registered consuming cactus fruits from September 2018 to July 2019 at a Caatinga site in Lajes municipality, Rio Grande do Norte State, northeastern Brazil. Cells are filled with the number of records. Number of frugivory records = 203.

Taxa	Species	<i>Melocactus zehntneri</i>	<i>Pilosocereus gounellei</i>	<i>Pilosocereus pachycladus</i>	<i>Cereus jamaicaru</i>	Total
AVES						
Columbidae	<i>Columbina picui</i>			9		9
Icteridae	<i>Icterus jamaicaii</i>			10	13	23
	<i>Molothrus bonariensis</i>			1		1

Picidae	<i>Colaptes campestris</i>		1*			1
	<i>Colaptes melanochloros</i>			2	2	4
Psittacidae	<i>Eupsittula cactorum</i>		7	12	14	33
	<i>Coereba flaveola</i>				4	4
Thraupidae	<i>Coryphospingus pileatus</i>	1		1	2	4
	<i>Paroaria dominicana</i>		4	1		5
Turdidae	<i>Turdus rufiventris</i>		7	9	7	23
	<i>Turdus amaurochalinus</i>				1*	1
Tyrannidae	<i>Pitangus sulphuratus</i>			5	3	8
	<i>Empidonomus varius</i>			7*		7
MAMMALIA						
Callitrichidae	<i>Callithrix jacchus</i>			1	13	14
Caviidae	<i>Kerodon rupestris</i>		2*			2
Echimyidae	<i>Thrichomys laurentius</i>		1*			1
Phyllostomidae	Bat			1		1
Small mammal	Non-identified		1			1
Canidae	<i>Cerdocyon thous</i>	2*	1			3
REPTILIA						
Gekkonidae	<i>Lygodactylus klugei</i>				1*	1
Tropiduridae	<i>Tropidurus hispidus</i>	18	30		1*	49
	<i>Tropidurus semitaeniatus</i>		6			6
Teiidae	<i>Salvator merianae</i>		2*			2
Total		23	21	62	59	203

* = new frugivory record on cacti species.

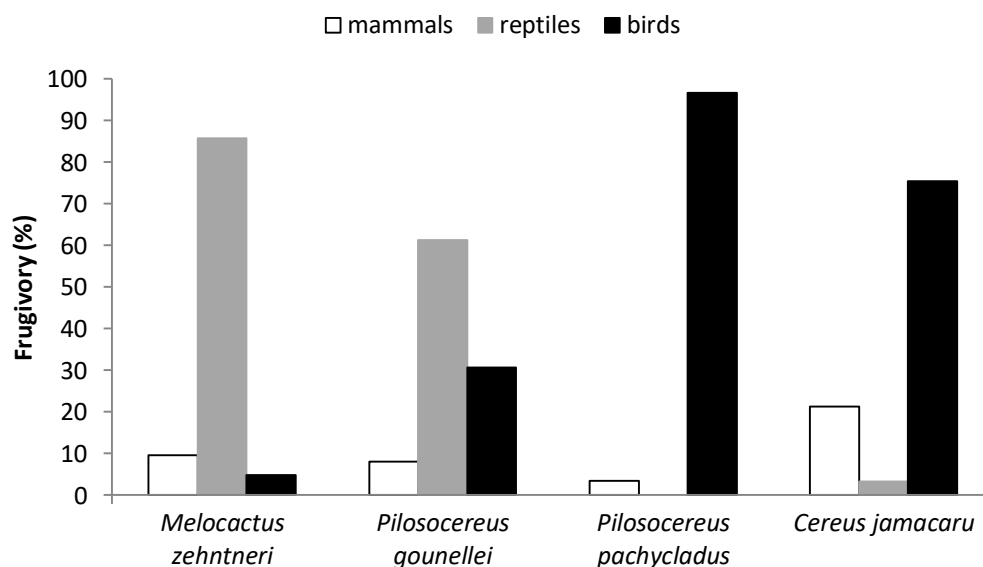


Figure 5. Percentage of frugivory (number of frugivory records per animal class divided by the total number of interactions each cactus had) recorded from September 2018 to

July 2019 at a Caatinga site in Lajes municipality, Rio Grande do Norte State, northeastern Brazil.

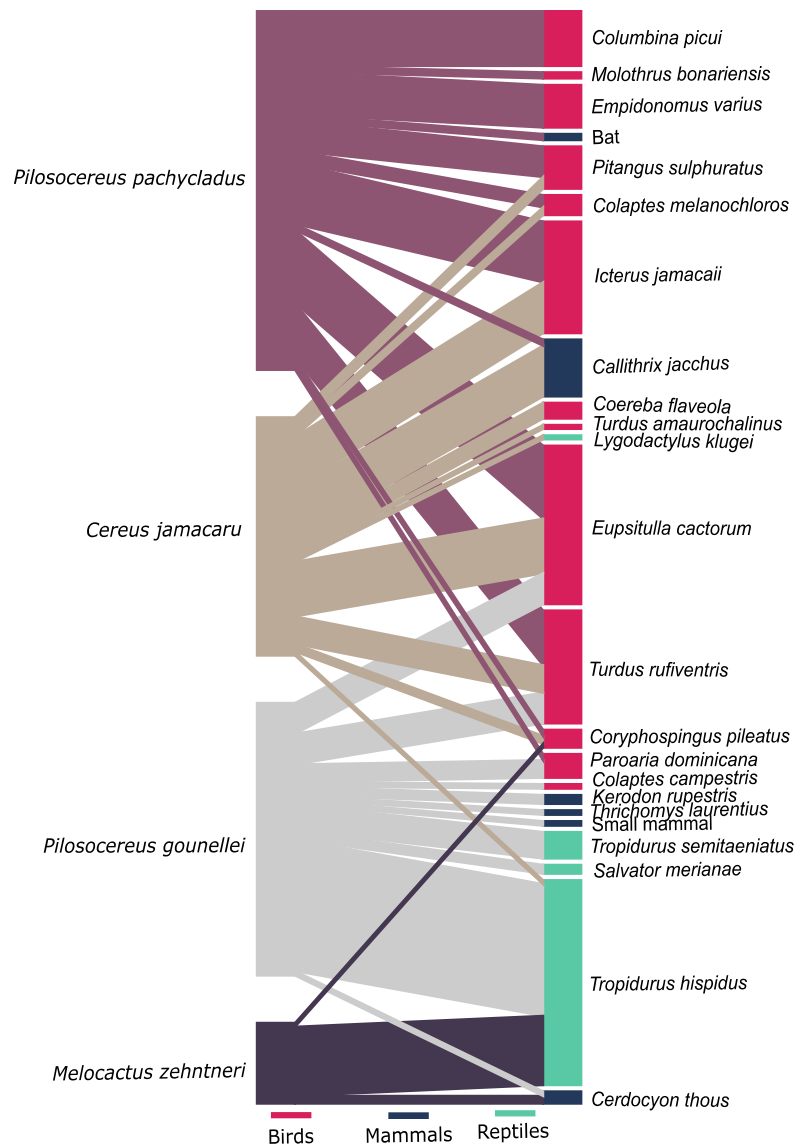


Figure 6. Quantitative cacti seed dispersal network by vertebrate frugivores. Data collected at a Caatinga site in Lajes municipality, Rio Grande do Norte State, northeastern Brazil, from September 2018 to July 2019. Cacti species are in the left boxes and vertebrate frugivores are in the right boxes. The links represents the interactions ((N° of frugivory interactions/sample effort (camera-days)*100).

Reptiles were responsible for ~ 86% of all frugivory interactions with the globular *M. zehntneri* (N = 21), all made by the terrestrial lizard *T. hispidus* (N = 18) (Tab. 4, Fig. 5, Fig. 7H). In all these fruit consumption events, *T. hispidus* was seen eating the fruits on the cactus or at the ground, biting and eating the whole fruit until it was completely eaten or it would bite it repeatedly times. In some of the frugivory events, these lizards were seen visiting *Melocactus* right after the fruit being extruded from the cephalium. After fruit consumption, the animal most of the times left the cactus. In some cases, they visited *Melocactus* on a daily basis, twice a day, in about the same time, that coincides with the day time that fruits of *Melocactus* appeared to be extruded in our cameras, that is in the morning (7-10:30h) and in the afternoon (15-16:30h). Even when there were no fruits, *T. hispidus* would stand up on this cactus apparently to thermoregulation, but they were also seen biting the cephalium. Mammal interactions with *M. zehntneri* accounted for 9.5% of total of interactions this cactus had, made by the Canidae crab-eating fox (*Cerdocyon thous*), a new report (Fig.6, 7G). We also had a record of insectivorous-granivorous Pileated Finche *Coryphospingus pileatus*.

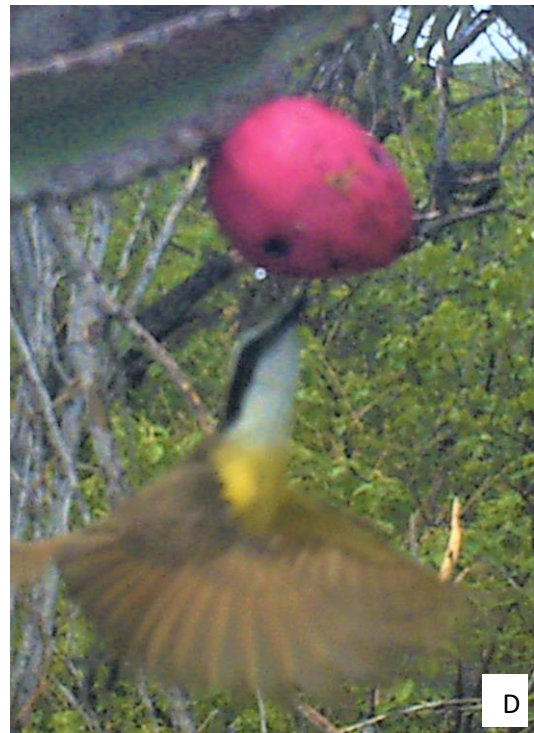
About 61% of the frugivory interactions with columnar *P. gounellei* (N = 62) were made by lizards (Fig. 5) and generalist *T. hispidus* alone was responsible for 48% (N = 30) of the interactions (Tab. 4, Fig. 7J). It was the cactus that interacted with a larger number of lizard (S = 3) and mammal (S = 4) species (Tab. 4). Among the lizards, *P. gounellei* interacted exclusively with the Tropiduridae *T. semitaeniatus* and the Teiidae *Salvator merianae* (Fig. 6, 7K), and among the mammals with the Caviidae rock cavy *Kerodon rupestris* (Fig. 6, 7F), the Echimyidae punaré rat *Thrichomys laurentius*, a non-identified small mammal, and also with *C. thous* (Fig. 4, Fig. 6). As for the birds, *P. gounellei* interacted exclusively with the Picidae *Colaptes campestris*,

and frequently with the frugivorous Cactus Parakeet *E. cactorum* and the Turdidae Rufous-bellied Thrush *Turdus rufiventris* (Tab. 4, Fig. 6).

About 97% (N = 57) of the frugivory interactions with *P. pachycladus* (N = 59) were with birds species. It interacted more frequently with Cactus Parakeet (Fig. 7A), Icteridae Campo Troupial *I. jamacaii*, and *T. rufiventris*, similar to the other columnar cacti (Tab. 4, Fig. 6). It interacted exclusively with Columbidae *Columbina picui* (Tab. 4, Fig. 6) which visits and consumption events were made by a couple of individuals with visits lasting an average of three minutes. Other exclusive interactions were with Tyrannidae *Empidonomus varius* (seven records) and one time with Picidae *Molothrus bonariensis* (Tab. 4), which are considered migrant species in the Caatinga (Araujo 2008). Beside the interactions with birds, it had two frugivory interactions with mammals (Tab. 4): the arboreal primate *Callithrix jacchus*, who had scaled to the top of the cactus branch to reach the fruit that was at about 4 meters high and a night frugivory event by a bat, which characteristics of the flight and uropatagium form are similar to those in nectarivorous bats (Fig. 6).

Most of the frugivory interactions (~ 75%, N = 46) with *C. jamacaru* (N = 61) were made by birds (Tab. 4, Fig. 5) (mainly *I. jamacaii* (Fig. 7B), *E. cactorum*, and *T. rufiventris* (Fig. 7C), followed by Primates (*C. jacchus*). It had exclusive interactions with *Coereba flaveola*, all marked by the quick duration of the visits, and with the migrant *Turdus amaurochalinus* (Tab. 4, Fig. 6). *C. jamacaru* was the species that had more interactions (in numbers) with mammals, all performed by the Primate *C. jacchus*, usually in groups of two to four individuals, while consumption of the fruit was accomplished by no more than two individuals at the same time. They held onto the fruit, while “punched” the inside of the pulp, grabbing it and taking it into the mouth to eat, otherwise they would put their head inside the fruit and directly ate the pulp with

the mouth (Fig. 7F). In both processes, they accidentally dropped part of the pulp fruit with seeds on the ground. Two lizard species consumed *C. jamacaru* fruits. The Tropiduridae *T. hispidus*, which stood on the fruit itself and was seen eating and dropping parts of the fruit pulp (Fig. 7I). The fruit had opened two days ago and it was first consumed by the bird *I. jamaicae*. This same fruit of *C. jamacaru* was also eaten by another lizard, *Lygodactylus kluzei*, a small (> 3 cm) arboreal Gekkonidae, a visit that lasted about 22 minutes. In this case, this small lizard stood on the thick fruit pericarp and was seen eating the fruit from the border. It is possible that it was eating small insects but due to the time the visit lasted it is very likely that it had swallowed the small seeds of *C. jamacaru* (>3 mm, Table 1) accidentally. The frugivory interactions between these two lizards and *C. jamacaru* are new reports for the cactus and for the diet of those animals.



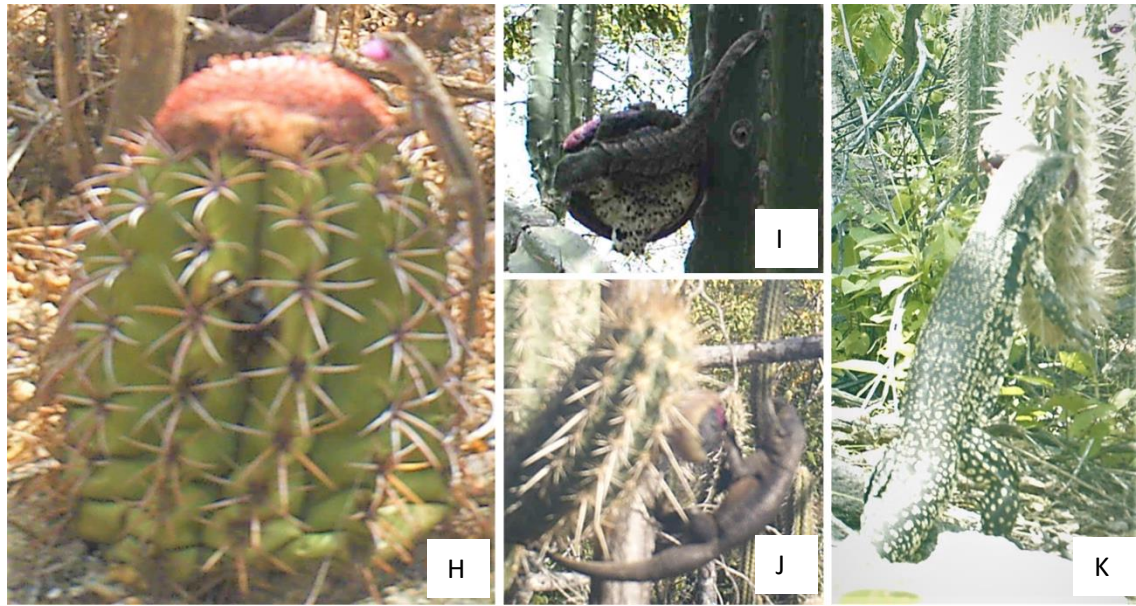


Figure 7. Frugivory records with camera-traps on cacti species at a Caatinga site in Lajes municipality, Rio Grande do Norte State, northeastern Brazil. A) *Eupsittula cactorum* on a *Pilosocereus pachycladus* fruit. B, C, D, E) *Icterus jamacaii*, *Turdus rufiventris*, *Pitangus sulphuratus*, and *Callithrix jacchus* eating *Cereus jamacaru* fruits. F) *Kerodon rupestris* eating *Pilosocereus gounellei* fruit. G) *Cerdocyon thous* eating a fruit of *Melocactus zehntneri*. H) *Tropidurus hispidus* with a *M. zehntneri* fruit on its mouth. I) *T. hispidus* eating *C. jamacaru* fruit. J) *T. hispidus* in *P. gounellei* fruit, K) *Salvator merianae* eating a *P. gounellei* fruit.

Patterns of frugivory

Bray-Curtis index showed that globular *M. zehntneri* was less different from *P. gounellei* (B-C = 0.42) when compared to the other columnar cacti *P. pachycladus* (0.02) and *C. jamacaru* (0.05). In turn, *P. gounellei* was equally different from the other columnar cacti species – *P. pachycladus* (0.21) and *C. jamacaru* (0.24). The higher columnar cacti, *P. pachycladus* and *C. jamacaru* held the higher value of B-C (0.55), meaning that they share a similar composition and number of interacting animal species.

We observed significant difference in the mean height that birds ($\bar{x} = 2.8$ m), mammals ($\bar{x} = 1.7$ m), and reptiles ($\bar{x} = 0.9$ m) ate cacti fruits (Kruskal-Wallis, p value < 0.001). In average, we had birds eating fruits in higher heights (fruits of columnar cacti),

mammals eating moderate high fruits and reptiles eating the lowest fruits (fruits of *M. zehntneri* and *P. gounellei*) (Fig.8). Even so, we had birds eating very low fruits (*C. pileatus* in *M. zehntneri*), mammals eating high fruits (*C. jacchus* in *P. pachycladus*) and reptiles eating fruits in moderate height (*T. hispidus* and *L. klugei* in *C. jamacaru*) (Fig. 9).

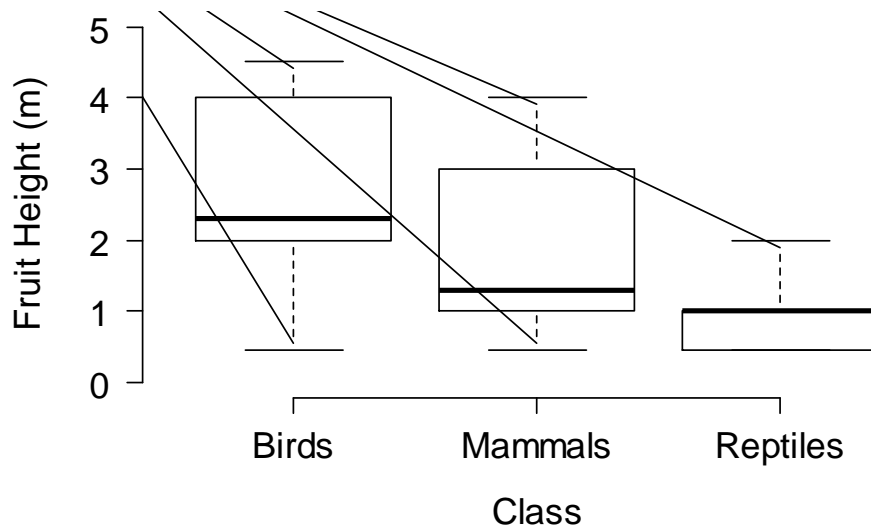


Figure 8. Height (m) of fruits consumed by birds (birds (N: number of records = 123), mammals (N = 22), and reptiles (N = 58)) of the four cacti species consumed from September 2018 to July 2019 at a Caatinga site in Lajes municipality, Rio Grande do Norte State, northeastern Brazil. Data about the following cacti species: *Melocactus zehntneri*, *Pilosocereus gounellei*, *Pilosocereus pachycladus*, and *Cereus jamacaru*.

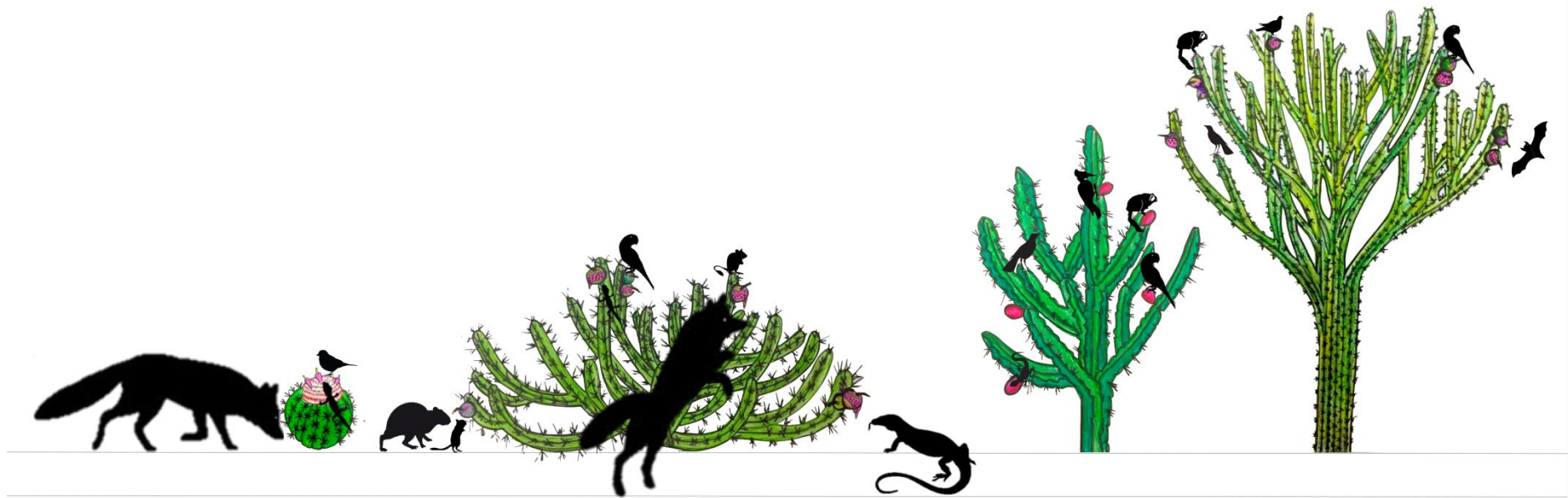


Figure 9. Illustration of the cacti community and its vertebrate frugivores represented by birds, lizards, and mammals. From right to left, in order: *Melocactus zehntneri*, *Pilosocereus gounellei*, *Cereus jamacaru*, and *Pilosocereus pachycladus*. See table 1 for mean fruit height for each cacti species.

Occasional records

We had a record on a Lepidoptera of the Sphingidae family with *P. pachycladus*. This insect was seen landing on a fruit at night. Other insects from the Lepidoptera order, specifically butterflies, were always seen on *C. jamacaru* fruits. Ants *Camponotus crassus* were always present in all cacti species and sometimes were visible in the cameras, but we didn't record them eating fruits or carrying seeds. We have seen ants of *Solenopsis* spp. species on camp eating the *P. gounellei* pulp, probably performing primary seed dispersal, and eating the *P. pachycladus* fruits pulp on the ground, possibly a form of secondary seed dispersal. We have also seen on camp field ants of *Atta* sp. carrying pulp and *M. zehntneri* seeds at night.

We recorded the Carnivore *Cerdocyon thous* eating *P. pachycladus* fallen fruits in two different occasions; also, we recorded it trying to catch *C. jamacaru* fruits at about 1.40 m height, although it was not possible to affirm if it has consumed the fruit. The *Mazama gouazoubira* deer was recorded walking around *M. zehntneri*, *T. inamoena* and *P. gounellei* with fruits available and accessible, but we did not record any frugivory interactions, as it has been reported that this animal feed on fleshy cacti fruits in the Chaco Boreal of Paraguay (Stallings 1984). Mammals such as *Euphractus sexcinctus* and *Conepatus amazonicus* were also seen near these previously mentioned cacti. The reptile *Ameiva ameiva* was frequently recorded foraging near *M. zehntneri*, in some cases there were fruits available on the cactus and on the ground, but there were no frugivory interactions between the pair of species. We had one record of frugivory interaction with the domestic goat, *Ovis aries*, eating globose *M. zehntneri* fruits which was excluded of the analyses due to its unnatural (domestic) presence at the study site. In despite of it, it has been found that domestic goats can disperse seeds of globular cacti species (*Echinocactus* spp. and *Ferocactus* sp.) in a semiarid thornscrub in Mexico

(Baraza and Valiente-Banuet 2008). We also recorded a male human individual taking an open ripe fruit of *C. jamacaru* with a wood stake.

Discussion

Frugivory records and network structure

We investigated the network structure and the frugivory patterns of cacti species in a semiarid environment. We observed cacti fruits consumption by a wide variety of animals, which might be an indicative that these plant species have a generalist seed dispersal strategy. Unlike our expectations nestedness and modularity were not significantly different from values generated by null models. For nestedness to occur in a network, it is necessary the existence of a network ‘core’, which is a relatively small group of highly connected species (Bascompte et al. 2003, Vázquez et al. 2009). In our network, all four cacti species, especially the columnar cacti (*P. gounellei*, *P. pachycladus*, and *C. jamacaru*) were responsible for forming the core of highly connected species, thus accounting for the entire network. In this scenario, there were not specialist plants, and all the frugivores, specialist or generalist, interacted with generalist cacti species. Nestedness is a consequence of interaction asymmetries and uneven distribution of interactions among species in the network (Bascompte and Jordano 2006). That said, we can infer that cacti-seed dispersal network interactions are less asymmetric and well distributed across the network. This also implies that cacti fruits are important food resources for animals that interact with them.

Seed dispersal networks formed by interactions among free-living species can fail to form the so called “long-term intimate mutualism”, as those of myrmecophyte–ant interactions (Fonseca and Ganade 1996, Guimarães et al. 2007), a mechanism that can strengthen modularity and lead to high compartmentalization (Olesen et al. 2007).

Because of that, modularity can be lower in seed dispersal networks, characterized by low interaction specificity, once plants often invest on the attraction of many frugivores as possible to increase the chances of its seed be deposited in a safe site favourable for growing a new individual (Howe 1993, Olesen et al. 2007). It is known that allocating many small seeds within a given fruit increases the potential diversity of dispersers by allowing small frugivores to ingest pulp pieces and seeds (Jordano 2000). We believe that this mechanism can be behind the non-establishment of modules in the cacti-seed dispersal network, once the cacti fruits investigated are characterized by the presence of many small seeds imbedded in a fleshy pulp, thus allowing the consume by many vertebrate species. This, in turn, can lead to a trade-off because when plants invest in fruit traits associated with the increase of partner diversity (e.g. fleshy pulp, small seeds), it can end up being consumed by non-mutualistic partners (seed predators, pulp peckers) (Fricke et al. 2017).

Our results show that *M. zehntneri*, *P. gounellei*, *P. pachycladus*, and *C. jamacaru* fruits are frequently used as food resource by many vertebrate frugivores. In *Pilosocereus* spp. seeds need to pass through vertebrate guts to remove the presence of secondary compounds present in the funicular pulp that reduce seed germinability (Meiado et al. 2012). Our data suggest that birds play a major role in fruit consumption and seed dispersal of columnar cacti in our study area, mainly *P. pachycladus* and *C. jamacaru*, where birds were the main consumers. This result is consistent to what was found in Brazilian arid areas, where Cactaceae was the most representative family on the diet of fleshy fruits of birds (Araujo 2009). In fact, the shape, colour and position of fruits of those species suggest that they evolved to be dispersed by birds (Soriano and Ruíz 2002). Here we found 13 bird species consuming cacti fruits, mainly those of columnar cacti. It is similar to the number of bird species consumers of columnar cacti

(*Stenocereus* spp., *Pilosocereus* sp. and *Cereus* sp.), varying from 8 to 19 species associated, in other Neotropical arid areas (Soriano et al. 1999). They share in common species of the families Picidae, Columbidae, Psittacidae, and Tyrannidae, also found in here, and which are considered the basic bird species composition in arid areas with extreme conditions (Soriano et al. 1999).

In relation to cacti seeds, Psittacidae and Columbidae species have been considered seed predators, while Tyrannidae (*Pitangus sulphuratus*) and Turdidae were considered seed dispersers, and *Coereba flaveola* was considered pulp eater (Soriano et al. 1999). Recent studies in Caatinga have pointed out the neglected mutualism between parrots and cacti, and the role of parakeets as cacti seed dispersers (Blanco et al. 2016). Thrushes are strongly frugivorous and have been described as the main dispersal agents in forested environments with high fruit availability (Jordano et al. 2007). Also, they perform flights dispersing seeds from tens to a few hundred metres, likely favouring the spatial aggregation observed in the study area (Breitbach et al. 2012).

In frugivory studies of columnar cacti in Caatinga of “Cariri Paraibano” in northeastern Brazil, seven bird species were registered consuming *P. gounellei*, five consuming *P. chrysostele* and nine consuming *C. jamacaru*, with *C. flaveola*, *I. jamacaii*, and *C. pileatus* in common with our records (Gomes et al. 2014, 2016, 2017). *C. pileatus* was the only bird species recorded consuming fruits of the globular *M. zehntneri*, which was also found in Cariri Paraibano (Araujo 2009) and in northeastern Venezuela (Poulin et al. 1994). Most of the bird families associated with cacti species in our study, with exception of Columbidae and Psittacidae, consumed fruits in quick visits, which is a desirable characteristic for effective seed dispersers, once long visits might increase the chances of birds defecating seeds under the mother plant (Pratt and Styles 1983). Bird species might be effective seed dispersers of columnar cacti in

Caatinga, where they can decrease germination time and defecate intact seeds (Gomes et al. 2014, 2017).

Reptiles played a major role in fruit consumption of columnar *P. gounellei* and globular *M. zehntneri*, mainly the Tropiduridae *T. hispidus*, but we also highlight the new record of *C. jamacaru* fruit consumption by *T. hispidus* and *P. gounellei* fruit consumption by the lizard Teiid *Salvator merianae* (see chapter 2). *T. hispidus* is known to be an effective seed disperser of *M. zehntneri*, while *T. semitaeniatus* is an effective seed disperser of *P. gounellei* and *Melocactus ernestii* (Gomes et al. 2013, Ferreira et al. 2016, Gomes et al. 2016, 2017). In general, saurochory has been pointed out as a distinctive dispersal mode in the Caatinga (Leal et al. 2017). The relationship between globular cactus and lizards is expected because *Melocactus* spp. are small cacti growing near the ground, facilitating the access by lizards, and there seems to be an adjustment in fruit release time and lizard activities, as well as a trait match between fruit characteristics (colour, claviform berries, proximity to the ground) and saurochory syndrome characteristics (Figueira et al. 1994, Vasconcellos-Neto et al. 2000, Fonseca et al. 2012, Gomes et al. 2013). Relationship among *Melocactus* spp. and lizards have been reported to be a positive evolutive interaction (Guerrero et al. 2012). In *M. violaceus* from northeastern and southeastern Brazil, 100% of its fruits were consumed by lizards *Tropidurus torquatus*; in arid areas in Venezuela and Colombia the lizards *Ameiva provitae* and *Cnemidophorus lemniscatus* consumed 72.5% and 17.5%, respectively, of *M. schatzlii* fruits (Guerrero et al. 2012). In these two cases, seeds ingested by lizards germinated earlier than seeds with fruit pulp, and with *M. violaceus* only seeds ingested by *T. torquatus* germinated, in comparison to the control group (Figueira et al. 1994, Guerrero et al. 2012).

Melocacti fruits are mainly composed by water (85%), a valuable resource in arid and semiarid areas marked by a pronounced dry season (Guerrero et al. 2012). Also, in our records, *T. hispidus* always ate entire fruits of *M. zehntneri*, considered behaviour of legitimate seed dispersers (Jordano 2000). This same behaviour could not be played by this same lizard to *P. gounellei* fruits, because its fruits are larger and has a large amount of pulp in comparison to melocacti fruits. In fact, in one of the records, one single fruit of *P. gounellei* was eaten many times by different lizards individuals in a single day, in one extreme case there were two lizards at the same time eating the same fruit. In addition, the dispersal services provided by the lizards recorded here are complementary - while *T. hispidus* can provide short-distance dispersal (6.5 ± 3.0 m) (Gomes et al. 2016), *S. merianae* can disperse seeds over longer distances as it walks through larger areas in search for food (see references in chapter II).

A relative wide range of mammals ate cacti fruits, including rodents, primates, bats and carnivores, potentially different in their seed dispersal effectiveness. Rodents are a poorer agent in the dispersal and recruitment of seeds, than birds and bats, due to the chewing and cracking (Janzen 1971). They can severely damage cacti seeds or completely destruct them, as found in the columnar cactus *Pilosocereus leucocephalus* and the rodent Mexican deer mouse (*Peromyscus mexicanus*) in Veracruz, Mexico (Vázquez-Castillo et al. 2019). Mammalian carnivores with generalist diet such as *C. thous* are medium-to-large-sized dispersers (1-7 kg) and occupy large home ranges which can include forests, open areas and farmlands, thus having the ability to disperse seeds over long distances (1–2 km) (Escribano-Avila et al. 2014, Dias and Bocchiglieri 2016). Crab-eating fox act as secondary seed dispersers in Brazilian rain forest, consuming fruits fallen to ground (Cazetta and Galetti 2009). They also can eat and disperse *P. gounellei* seeds, slowing their germination rate, as found at the Caatinga of

Sergipe State (Dias and Bocchiglieri 2016, Souza 2019). It is not clear if in the aforementioned cases, *C. thous* have consumed cacti fruits from the ground or from the tree; which in this sense our records highlight the role of crab-eating foxes as primary seed dispersers of *M. zehntneri* and *P. gounellei*. In general, medium-sized mammals have been considered a key element in the regeneration of old, abandoned fields, what is crucial in front of our increasingly land use and abandonment in the Caatinga (Escribano-Avila et al. 2015).

The role of bats was little (one quick visit) when compared to the other animals that interacted with cacti, despite several studies reinforcing the role of bats as effective seed disperser of columnar cacti (Soriano et al. 1991, Naranjo et al. 2003, Soriano and Ruíz 2002, Valiente-Banuet et al. 2002). At our study area, in another study about bats, from about 600 individuals of frugivorous bat *Artibeus planirostris*, only 2% had *P. pachycladus* seeds in their faeces (Juan Carlos Vargas-Mena, personal communication). In a study about the bats' diet in Caatinga of Pernambuco State, Brazil, from 18 bat species, only one (*Glossophaga soricina*) ate cacti fruits (*P. pachycladus*) (Silva 2007). In another Caatinga area in "Cariri Paraibano", cacti fruits consumption (*C. jamacaru*, *P. gounellei*, and *P. chrysostele*) by bats were not found (Gomes et al. 2014, Gomes et al. 2017), despite observations at night been carried out. Despite our equal daytime and nighttime sample effort, we found little bat-cacti interactions of seed dispersal, which may be an indicative that those interactions have already been lost. At our study site, bats are active through the night where they forage on cacti flowers for nectar (Cordero-Schmidt 2016). It is possible that for the cacti system studied here, bats play a major role as pollinators, while birds act as seed dispersers of columnar cacti.

The absence of interactions with the cactus *T. inamoena* species could be a result of the local extinction of its former seed dispersal agent, such as peccaries, due to

anthropic disturbance (Machado and Taylor 2003, Lambert 2009, Marinho et al. 2018, 2019). Valient-Banuet et al. (2014) argue that the loss of interactions can occur before species disappearance. It also can be related to the glochids present in the fruits, as it can remain until after the ripe fruit fall to the ground (Menezes et al. 2013). In spite of it, the bird species *Cyanocorax cyanopogon* has been visually observed eating fruits in an area of Caatinga in Paraiba state, Brazil (Araujo 2009, also see chapter 2). Also, seeds of *T. inamoena* have been found in parakeets and parrots' faeces in Caatinga (Blanco et al. 2016). In species of the subfamily Opuntioideae, such as *T. inamoena*, vegetative reproduction is prominent, where the jointed stem-segments can be detached, carried and form roots when in contact with the ground (Taylor and Zappi 2004).

Patterns of frugivory

Our data did not show a modular pattern for the network of cacti-seed dispersal by vertebrates, but we observed a distinction in how animal community interact with cacti resources. In this way, we highlight that cacti with similar height share similar species composition and number of interactions, higher cacti are consumed by more mobile animals (birds, bats, arboreal primates), while lower cacti are consumed by less mobile animals (reptiles, non-flying mammals). Namely: columnar cacti *P. pachycladus* and *C. jamacaru* are mainly consumed by birds and arboreal primate, and columnar *P. gounellei* and globular *M. zehntneri* are mainly consumed by reptiles and non-flying mammals.

Despite *P. gounellei* bearing fruits with ornitochory characteristics (e.g. small seeds, purple pulp), similar to *P. pachycladus*, because some of its fruits are set closest to the ground, it can be accessed by a higher diversity of animals, mainly reptiles, followed by birds and mammals. One can argue that a lizard such as *T. hispidus* is capable of climbing cactus branch to reach fruits of *P. pachycladus* on the top (at

heights over 4 m) but Falconidae southern caracara (*Caracara plancus*) uses the taller cactus for perches, the exposure of *Tropidurus* when climbing these branches represents a potential risk. Also, a bird could potentially consume *M. zehntneri* fruits, as they can virtually access fruits at any height, but in the case of *Melocactus*, its fruits (lilac coloured) can be less conspicuous to birds (Taylor 1991).

Generalization can benefit plants by increasing the spectrum of dispersers which in turn can increase the probability of seeds being deposited in an adequate site for recruitment (Schupp et al. 2010). Modularity can increase network robustness as disturbances will spread more slowly across compartments (Tylianakis et al. 2010, Stouffer and Bascompte 2011). Conversely, highly modular networks are also little connected, which can decrease redundancy and robustness against extinctions (Dehling 2018). Seed dispersal networks in large (Neotropics, Afrotropics) and local scales, involving birds and/or bats and plants, palm trees and frugivorous animals, or plants and animals in general in semiarid Mediterranean and in Brazilian Pantanal have shown both modular and nested pattern (Donatti et al. 2011, Muñoz et al. 2018, Acosta-Rojas et al. 2019, Oliveira et al. 2019). In Brazilian Cerrado, a seasonally dry ecosystem, modularity and nestedness did not occur in a network between fleshy fruited plants and small mammals (Genrich et al. 2017). Our cacti-seed dispersal network also did not show modularity and nestedness, although frugivores recorded consuming cacti fruits differ in morphology and behaviour, therefore they may contribute in a complementary, non-redundant way to cacti seed dispersal (Escribano-Avila et al. 2014).

At Caatinga sites, including our study area, it is a common practice cutting and burning *Pilosocereus* and *Cereus* branches to livestock feeding, especially during the drought. Also, cacti species are often cut just to “clean” the area, and are generally seen as “less valuable” by local communities. These practices have systematically decreased

cacti density, and considering that droughts are becoming more frequent, it is expected that the pressure over cacti populations will increase. Our study, in turn, draws attention to the relevance of cacti fruits as a resource for a wide variety of vertebrates, where some expected interactions no longer occurs. Therefore, we reinforce the need to protect and conserve cacti species.

Conclusions

Cacti offer fruits continuously throughout the year and support a network with animals that use them as food resources, maintaining a resident frugivorous fauna. In addition to birds, it is possible that reptiles and mammals also play a distinctive role in cacti seed dispersal, although seed dispersal efficiency studies should be carried out. For natural regeneration, it is crucial to maintain ecological services provided by functionally diverse of animal seed dispersers and this should be taken in account in conservation actions that aim to restore Caatinga areas dominated by cacti species. Such is the case of Lajes municipality, which holds the largest continuous fragment of Caatinga in Rio Grande do Norte State, and its high abundance of cacti holds a unique fauna. Despite the relevance of this municipality, it lacks the existence of legally protected areas. In addition, Lajes is targeted by wind power companies, apart from being subjected to livestock and deforestation. Our results reinforce the necessity of protecting this region, along with its species and interactions, in order to maintain its integrity.

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Supplementary material

I – Local rainfall during the study period

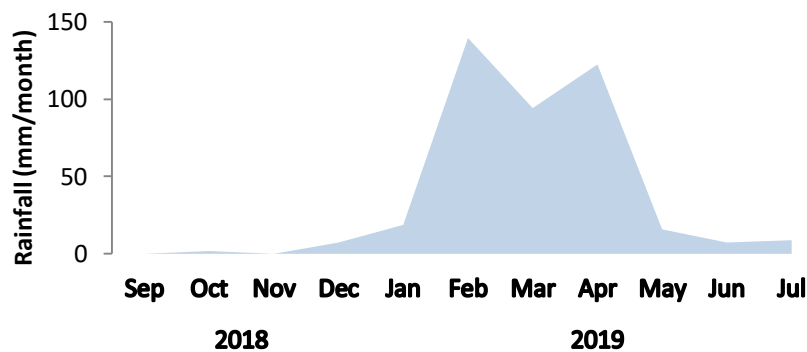


Figure 4. Lajes municipality rainfall, Rio Grande do Norte State, northeastern Brazil. Data available in Empresa de Pesquisa Agropecuária do Rio Grande do Norte – EMPARN from September 2018 to July 2019.

II - Biological information about cacti species studied

The size, shape, and pulp colour of fruits of *Pilosocereus* spp. and *Cereus* spp. favour chiropterochory and ornithochory (Soriano and Ruíz 2002). These fruits dehisce at maturity attracting birds with the bright colour of its purple and white pulp (Taylor and Zappi 2004). Another characteristic related to those mechanisms of seed dispersal is to set fruits at the top of the branch, which is also a general behaviour in columnar cacti (Soriano and Ruiz 2002).

Fruits of *Melocactus* spp. develop inside the cephalium, a modified portion of the stem made of wool and bristle that serves to protect the developing flowers and unripe fruits (Machado 2009). When ripe, fruits are expelled from the cephalium, usually in the morning or soon in the afternoon, when they become available upon the cactus and many fall onto the ground beside the cactus; fruits characteristics are related to saurochory, what makes lizards its commonest local dispersal agents (Figueira 1994, Fonseca et al. 2012). *M. zehntneri* produces fruits of a lilac-pink colour, which can be less conspicuous to some dispersal agents such as birds (Taylor 1991).

Tacinga inamoena (former *Opuntia inamoena*) fruits, similar to in *Opuntia* spp. seems to hit maturity only when fall to the ground (Nobel 2002, Taylor and Zappi 2004). It differs from the other cacti species due to the lack of spines and the presence of glochids, which consists of bristles from 3 to 6 mm long that can cause injury when in contact with the skin (Schreiber 1971). Glochids are very abundant, present in areoles spread over the cladode and in the flower and fruit pericarp, which some, in this last one, can be lost when fruit hits maturity in some *Opuntia* species (Menezes et al. 2013, Lloret-Salamanca et al. 2015). The loss of glochids would facilitate the fruit ingestion and seed dispersal by animals, which for *Tacinga* were formerly related to mammals such as peccaries, which are absent from many Caatinga areas due to antropogenic pressures, such as illegal hunting and deforestation (Taylor and Zappi 2004, Marinho et al. 2018, 2019).

Chapter II: Interactions between lizards and cacti in the Caatinga



General introduction

Plants and animals interact in many different ways. Interactions can be mutualistic, when plants and animals benefit from it, such as seed dispersal interactions, or antagonistic, when one of the parts loses, such as herbivory (Dáttilo and Rico-Gray 2018). In the past few years, studies showed that lizards are involved in a mutualistic way with Cactaceae species in Caatinga (Leal et al. 2017). They can act as seed dispersers of cacti species, not only the globular ones, such as from *Melocactus*, but also from columnar cactus such as *Pilosocereus gounellei* (Gomes et al. 2013, 2016). An example of double mutualism was also found between lizards and *Melocactus*, where these animals were seen pollinating flower in addition to eating fruits (Gomes et al. 2013). In a lesser extent, lizards are involved in antagonistic relationship with cacti, as they were seen preying *Melocactus* flowers (Gomes et al. 2013). In seasonal ecosystems with low water availability, lizards are attracted to cacti resources such as flowers and fruits, which are sources of water and nutrients (Guerrero et al. 2012). Yet, more research on the basic ecology of plant-animal interactions in the Caatinga is still needed.

This chapter reports interactions as *short communications* between lizards and cacti from Caatinga. Such interactions are part of a bigger scenario where cacti-animal interactions were accompanied during one dry and rainy season in the Caatinga. In this way, the first report is about an antagonistic interaction where lizards were recorded eating cactus flowers. The second is a mutualistic interaction of cactus fruit eating by a lizard and its potential as seed disperser, and it was written following Studies on Neotropical Fauna and Environment formatting guidelines for *short communications*. Such case studies are required to increase the knowledge about Caatinga interactions and might help us unveil singularities of this Neotropical seasonally dry forest.

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Lizard florivory on the prickly pear *Tacinga inamoena* (Cactaceae) in the Brazilian Caatinga

Introduction

Florivory is related to the consumption of floral structures by a wide variety of animal taxa (McCall and Irwin 2006). It can decrease the reproduction success of a plant by damaging the floral sexual structures and altering flowers availability to pollinators (Cascante-Marín et al. 2009). In Cactaceae family, florivory have been found especially in drier areas, where cacti flowers stand out for their water content and nutritional value (Nobel 2002). In such environments, cacti flowers are partially or entirely consumed by invertebrates, such as *Opuntia* flowers eaten by Lepidoptera larvae in Chihuahuan Desert (Pinã et al. 2010), and vertebrates, such as *Opuntia* flowers eaten by lizards in Galapagos Island (Nobel 2002), and *Melocactus* flowers eaten by Tropiduridae lizards in the Brazilian Caatinga (Gomes et al. 2013), and the short columnar cactus *Echinopsis rhodotricha* florivory by deer and peccary (Gomes et al. 2016).

Generally, vertebrate florivory distinguishes from invertebrate florivory in a way that in the first case, flowers are often entirely eaten (Riba-Hernandez and Stoner 2005). Such is the case of florivory by lizards, as their feeding on flowers is often destructive (Olsson et al. 2000, Gomes et al. 2014). Many lizard species feed on nectar and other flowers parts because of their nutritional and energy value, potentially playing a significant role in pollen transfer (Pérez-Mellado and Casas 1997). Florivory by lizards is common among iguanines (Iverson 1982) and have been observed in islands and in the mainland, as the case of Cactaceae *Opuntia* flowers eaten by teiids and terrestrial iguanines (Christian et al. 1984, Mijares-Urrutia et al. 1997).

Among cacti species, *Tacinga* Britton & Rose 1919 is a genus of the subfamily Opuntioideae, composed by prickly-pear cactus endemic from Brazil, which only occurs in the semiarid lands in the Eastern corner of the country (Lambert 2009). *Tacinga inamoena* (K.Schum.) N.P.Taylor & Stuppy is a subshrub cactus which flowers have a globose pericarpel, 10 mm, green, with orange-red, acute, fleshy bract-scales subtending bristles (Taylor and Zappi 2004) (Appendix A, Fig. 1A). Their flowers are the showiest of the genus, which are large and shiny with erect stamens forming a column surrounding the stigma, pollinated by hummingbirds (Lambert 2009). Their flowering period starts at the end of the rainy season, continuous along all the dry season, with a peak in September/October (Quirino 2006).

Tropidurus hispidus is a heliophilous generalist lizard that can reach up to 32 cm length, the largest of the genus (Kolodiuk et al. 2010). It is widely distributed in South America, including open landscapes such as Caatinga, living in forest borders, rock outcrops, and human altered areas (Fialho et al. 2000). Its diet can comprise mainly plant material in the dry and rainy seasons (leaves and non-identified flowers) but also ants and insect larvae at Caatinga areas (Albuquerque et al. 2018, Kolodiuk et al. 2010, Van Sluys et al. 2004). These studies reinforced the role of *T. hispidus* as flower consumers, although no attention has been given to the identity of the flower species.

During a study on Cactaceae frugivory by vertebrates at a Brazilian tropical dry forest called Caatinga, we recorded florivory events by *T. hispidus* on *T. inamoena*, which are new information for both species.

Material and methods

Field work was carried out in a private property called Fazenda Santo Antônio located in Lajes municipality (S05°47'48.4" W036°14'23.8"), in Rio Grande do Norte

state, in the semiarid region of northeast Brazil. The region is characterized by a low irregular rainfall (>300 mm/year), long periods of drought, and high average annual temperatures (30 °C). We monitored 11 *T. inamoena* individuals from September 2018 to July 2019 for potential fruit/flower consumption, totalling 450 camera-days of sample effort, distributed throughout the months, and around 53 flowers monitored. Monitoring was carried out with camera traps (Bushnell Trophy CAM 8 MP HD) placed one to two meters away from the cactus. We configured the cameras to capture 2 photos followed by a 10 seconds video, in intervals of one minute. We then left the cameras in the field working 24 hours/day for a month. We chose plants away from each other at least 70 m to ensure spatial heterogeneity.

Results and discussion

T. hispidus ate four *T. inamoena* flowers, what corresponded to 7.5 % of the flowers monitored in the study period. Three of the florivory events happened in the same cactus individuals, but in different days. The events occurred during the morning, three of them in the end of the dry season in 2018 (Nov-Dec), and one in the rainy season of 2019 (Apr) (Tab. 1). It is probable that the florivory events in the same cactus were performed by the same lizard individual due to the similarities of the organism, what is not the case of the fourth florivory event, that occurred more than 70 m away from the previous one, and this distance is larger than the home range of *T. hispidus* (Melo et al. 2017). Also, there were clear differences individual sizes, one being bigger than the previous.

The lizards approached the plant and started eating the flowers, which were all located near the ground level, beginning by tearing the petals until reach the globular structure, without climbing the cactus. The flowers were eaten gradually in single visits

that in some cases lasted several minutes (Tab. 1). In three of the events the globular part was almost entirely eaten, while in only one the petals were not fully eaten and a little damage was caused to the globular part. After that, it was not observed visits from pollinators to the remnants petals, as we observed visits by hummingbirds in intact flowers when they opened. *T. inamoena* flowers take about 25 days to open, and stay open for a day or two at most. The lizards were seeing predating *T. inamoena* flowers right after anthesis, presumably because these have the greatest amount of nectar, which is also the brief period the cactus has to interact with pollinators.

The complete removal of the flower takes away the chances of its reproduction and the probability of generating a fruit. Also, petal removal can indirectly decrease reproductive output via decreased flower visits by pollinators (Tsuji and Ohgushi 2018). In *Opuntia* sp., florivory by Lepidoptera larvae caused a substantial decrease in their reproductive success (Pinã et al. 2010), likewise, in the short columnar cactus *E. rhodotricha* no fruits developed in flowers damaged by deers and peccaries in the Brazilian Chaco (Gomes et al. 2016). Flower eating by *T. hispidus* was observed in populations of Caatinga and Cerrado, which was higher during water scarcity periods at dryer areas (Albuquerque et al. 2018). The search for flower food is due to not only the need of water but due to its high level of nutrient contents, especially in environments where water and food resources are in short supply in the dry months, which can correspond to a great part of the year. Additional investigation is needed in order to quantify the florivory in *T. inamoena* and to understand whether this is a selective pressure capable of influencing its reproductive success reducing the fruit and seed set.

Table 1. Day of *Tacinga inamoena* flower anthesis, day of flower consumption by the lizard *Tropidurus hispidus*, time of consumption (start time and end time), height of the

flower consumed (m) and geographic location of the cactus consumed at a Caatinga site in Lajes municipality, Rio Grande do Norte State, northeastern Brazil.

Anthesis	Consumption	Start time	End time	Flower height	Location
11/15/2018	11/15/2018	08:42	09:22	0.3	05°47'48.4" 036°14'23.8"
11/29/2018	11/29/2018	08:09	08:20	0.6	05°47'48.4" 036°14'23.8"
12/26/2018	12/26/2018	09:01	09:03	0.4	05°47'48.4" 036°14'23.8"
04/15/2019	04/16/2019	10:44	10:45	0.1	05°47'52.4" 036°14'21.3"



Figure 1. A) *Tacinga inamoena* flower, B and C) *Tropidurus hispidus* looking at an entire and partially eaten flower, respectively; D) *T. hispidus* jumping and eating the flower it was looking at C.

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Cactus frugivory by the lizard *Salvator merianae* (Squamata: Teiidae) recorded with cameras trap at Brazilian Caatinga

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Abstract

Salvator merianae is a lizard native to South America characterized by an omnivorous diet including fruits. Here we report the first record of primary seed dispersal by *S. merianae* at a Caatinga site in Northeastern Brazil. We assessed cacti frugivory by vertebrates through cameras trap sampling during eleven months. We recorded two frugivory events by *S. merianae* on the columnar cactus *Pilosocereus gounellei*. Lizards are known to disperse cacti seeds in Caatinga, and *S. merianae*'s could potentially offer

a long distance dispersal service as it walks through large areas while searching for food. This is a new report to *S. merianae* in the Caatinga ecosystem and contributes to display data about the fruit-eating diet and the potential role as seed dispersers of lizards which still remain to be discovered around the world.

Keywords: black-and-white tegu; Cactaceae, *Pilosocereus gounellei*; seed dispersal

Introduction

Salvator merianae (Black-and-white tegu) (Duméril & Bibron, 1839) is a Teiidae lizard native and widely distributed in South America, occurring in many Brazilian environments such as Caatinga (dry forest), Cerrado (savannah), and Atlantic Forest (rain forest) (Van Sluys 1999, Kiefer & Sazima 2002, Vieira et al. 2018). It is the largest species of its genus, reaching 1.2 m of total length and weighting over 4.5 kg (Milstead 1961, Fitzgerald 1992). The black-and-white tegu is known to have an omnivorous diet which includes invertebrates, vertebrates, eggs, and many types of fruits (Kiefer & Sazima 2002). This Teiidae belongs to one of the lizard families that have more registers of fruit consumption (Valido & Olesen 2007).

Despite advances in the study of *S. merianae*'s diet, most of the data available for the fruit eating diet of this large lizard comes from experiments where individuals are exposed to fruits or through stomach content analysis or traditional knowledge (Kiefer & Sazima 2002, Castro & Galetti 2004, Silva et al. 2014). From what we know, primary seed dispersal, which means when seeds are removed before it reaches the ground

(Muller-Landau & Hardesty 2005), by *S. merianae* is still unknown. Here we describe new records of the black-and-white tegu consuming fruits from the cactus *Pilosocereus gounellei* subsp. *gounellei* on nature at a Caatinga site in northeastern Brazil.

Materials and methods

Fieldwork was conducted at Lajes municipality, in a private property named Fazenda Santo Antônio, located in the central portion of Rio Grande do Norte State (05°47'55.5"S 36°14'22.2"W), northeastern Brazil. The region is characterized by Caatinga vegetation, with tree and shrub formations and a dry semiarid climate, marked by an extended dry season and erratic and unpredictable rainfall that usually occurs from February to May, when the total amount of precipitation reaches 350 mm (Szilagyi 2007, Brito et al. 2017, Tomasella et al. 2018).

We recorded vertebrate frugivory interactions with 17 *P. gounellei* individuals with camera traps (Bushnell 8 MP Trophy Cam), from September 2018 to July 2019, totalling 621 cameras-days. We set the cameras close (2–5 m) and toward a cactus fruit, and programmed to take two pictures followed by a 10 seconds video, in minimal intervals of one minute when triggered, and left in the field working 24 h per day to detected elusive, scarce or nocturnal potential frugivores (Blanco et al. 2019).

Results

We recorded two frugivory events on *P. gounellei* by *S. merianae* on 22 and 23 May 2019 at 1027 h and 1104 h respectively. By comparing the individual's morphology and colour patterns through images we observed that the consumption was made by the

same *S. merianae* individual. At the time of the frugivory record, there were two fruits available at 0.7 m height. In the records the animal ate the pulp from both fruits and for that it stood in bipedal position and used its hands to improve balance by touching the cactus spines (Fig. 1, video in supplementary material).

Discussion

Here we report the first records of fruit consumption of *P. gounellei* by *S. merianae*, as well as the first evidence of primary seed dispersal by this large lizard. *P. gounellei* is a shrubby columnar cactus that can reach up to 3 m height and is covered by thick spines of 150 mm length (Menezes et al. 2013). Its dehiscent fruits when mature expose its fleshy colourful funicular pulp with many ($N \leq 4000$) small (1x1 mm) black seeds embedded (Abud et al. 2012). *Pilosocereus* spp. funicular pulp can inhibit seed germination through the production of allelopathic substances, which reinforces the need of zoochoric vectors to remove this chemical barrier and promote seed germination (Meiado et al. 2012).

It has been shown that lizards can be an effective seed disperser of cacti species (Guerrero et al. 2012). *S. merianae* has been reported to consume fruits of the columnar cactus *Cereus jamacaru* at another area of Caatinga, which has a little participation in its diet and it is not known if the animals accessed the fruit fallen on the ground or in the tree (Silva et al. 2014). This Teiidae also chose to eat the cactus fruits of *Cereus peruvianus* when offered in a controlled experiment, but it did not affect the percentage and time of seed germination after the gut passage (Castro & Galetti 2004).

Despite being generalist, plant matter such as fruits and seeds can correspond to 50 % of *S. merianae*'s diet, thus it can potentially act as seed disperser, as it defecates

intact seeds and walk through large areas while searching for food (home range ≥ 4 ha) (Castro & Galetti 2004, Silva et al. 2014). *S. merianae* also differs from other cactus-seed dispersing lizards, such as *Tropidurus* spp., due to its bigger size and weight (1.2 m, 4.5 kg) (Fitzgerald 1992), and because they are not capable to climb the cactus to access fruits in high heights, being conditioned to access lower or fallen fruits.

This is a new report to *S. merianae*, evidencing that this species consumes fruits directly from the plant, generally fresher, and increasing the diversity of cacti's species that provide food for this lizard. Our work contributes to display data about the fruit-eating diet and the potential role as seed dispersers of lizards which still remain to be discovered around the world (Valido & Olesen 2019). It also contributes to the increasingly knowledge about the intimate relationship between Caatinga's lizards and cacti (Leal et al. 2017). Future works should evaluate the role of *S. merianae* lizards as effective cactus-seed disperser, an interaction that can be lost before it is known due to the intense poaching pressure this lizard suffers in Brazil semiarid region (Alves et al. 2012).

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Figure 1. *Salvator merianae* consuming *Pilosocereus gounellei* fruits at a Caatinga site in Lajes municipality, Rio Grande do Norte State, Northeastern Brazil.

Supplementary material

Link to frugivory record video: https://youtu.be/GmEkb6_cEA0