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UNIVERSIDAD DE CHILE - FACULTAD DE CIENCIAS - ESCUELA DE POSTGRADO

MECANISMOS DE DISPERSIÓN DE FRUTOS Y SEMILLAS EN DOS CACTÁCEAS COLUMNARES EN CHILE

Tesis entregada a la Universidad de Chile en cumplimiento parcial de los requisitos para optar al grado de Magíster en Ciencias Biológicas

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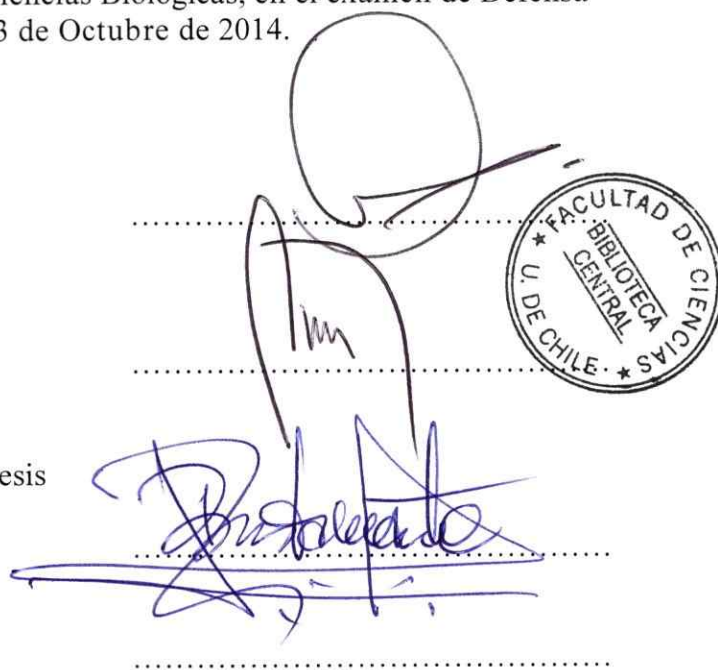
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The image shows a large, stylized handwritten signature in blue ink that spans across the dotted lines for the Director of Thesis, Co-Director of Thesis, and the Evaluation Commission. To the right of the signature is a circular stamp with the text "FACULTAD DE CIENCIAS" at the top, "BIBLIOTECA CENTRAL" in the middle, and "U. DE CHILE" at the bottom, flanked by two stars.

*“Todas las cosas por fuerza inmortal,
ocultamente, están ligadas unas a otras,
tanto que uno no puede tocar ni una flor
sin perturbar a una estrella”*

Proverbio Azteca

BIOGRAFÍA

Nací en La Serena el 13 de Octubre de 1987. A los 4 años llegué a Santiago, donde he realizado todos mis estudios. Primero la educación básica en el Colegio London, y el final de la básica y toda la educación media en el Complejo Educacional La Estrella, siempre en la comuna de La Florida. En el año 2006 ingresé a la Universidad de Chile a estudiar Biología Ambiental, carrera que me llevó a interesarme por el estudio y la conservación de la naturaleza. El año 2009 comencé a trabajar en el Laboratorio de Ecología Evolutiva, donde la Dra. Carezza y el Dr. Rodrigo me dejaron trabajar con plantas, que era lo que más me gustaba, específicamente con cactus, llegando a realizar mi tesis de pregrado y postgrado en esta misma área. A través de todos estos años, me he esforzado por llevar mi investigación hacia el estudio de la historia natural con enfoque en la conservación de las especies, esperando que esta tesis se transforme en un aporte al conocimiento de la flora de Chile.



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RESUMEN

La dispersión de semillas es un importante proceso ecológico ya que resulta en el reclutamiento y establecimiento de nuevos individuos, a través de la interacción con frugívoros que transportan las semillas a sitios donde la probabilidad de reclutamiento de plántulas es mayor, contribuyendo efectivamente a la reproducción de especies de plantas. En este estudio, realizado en la Reserva Nacional Las Chinchillas (31°30'S, 71°06'W), se estudiaron los mecanismos de dispersión de frutos y semillas de dos especies de cactáceas de Chile, *Leucostele chiloensis* (ex *Echinopsis chiloensis*) y *Eulychnia acida*, y se determinaron los frugívoros que actúan como dispersores de semillas, mediante observaciones de campo y experimentos de germinación en laboratorio. El fruto dehiscente de *L. chiloensis* se abre en el brazo del cactus al madurar, y siete especies de frugívoros pudieron ser identificados. Sin embargo, el ave *Mimus thenca* actuó como principal dispersor efectivo, depositando las semillas en sitios seguros para el establecimiento y aumentando la germinación. Por el contrario, el fruto indehiscente de *E. acida* cae por abscisión, y ningún dispersor de semillas fue detectado. Las características del fruto y la ausencia de frugívoros en esta población podrían estar dando cuenta de un síndrome de dispersión por megafauna. Evaluar el grado de dependencia entre animales y plantas es central para determinar los efectos que los dispersores de semillas tienen en el mantenimiento de las poblaciones naturales.

ABSTRACT

Seed dispersal is an important ecological process because it results in the recruitment and establishment of new individuals, through the interaction with frugivores that transport seeds to sites where the probability of seedling recruitment is high, contributing effectively to the reproduction of plant species. In this study, carried out in the Reserva Nacional Las Chinchillas (31°30'S, 71°06'W), it was studied the dispersal mechanism of fruits and seeds of two Chilean cactus species, *Leucostele chiloensis* (ex *Echinopsis chiloensis*) and *Eulychnia acida*, determining the frugivores acting as seed dispersers by field observations and laboratory germination experiments. The dehiscent fruit of *L. chiloensis* opens on the cactus branch when ripens, and seven frugivorous species were identified. However, the bird *Mimus thenca* acted as the main effective disperser, depositing seeds in safe sites for the establishment and increasing germination. In contrast, the indehiscent fruit of *E. acida* drops by abscission, and no seed dispersers were detected. Fruit characteristics and the absence of frugivores in this population may be accounting of megafaunal dispersal syndrome. To assess the degree of dependence between animals and plants is central to determine the effects that seed dispersers have on the maintenance of natural populations.

INTRODUCCIÓN

La dispersión de semillas es un importante proceso ecológico que consiste en la remoción y deposición de semillas lejos de las plantas parentales, lo cual resulta en el reclutamiento y establecimiento de nuevos individuos (Howe y Smallwood 1982, Willson y Traveset 2000, Godínez-Álvarez y col. 2002, Herrera 2002). En este proceso pueden estar involucrados tanto factores abióticos, como viento, agua, gravedad o autodispersión por explosión (Stoner y Henry 2008), como factores bióticos, que consisten en la dispersión a través de animales, involucrando mamíferos, aves, reptiles e insectos, a cuyos cuerpos las semillas se adhieren y son transportadas, o son ingeridas y dispersadas a través de la defecación (Herrera 1995, Jordano 2000, Casado y Soriano 2010). Los animales que ingieren los frutos juegan un papel fundamental en el transporte de las semillas desde los individuos parentales hacia sitios donde la probabilidad de germinación es mayor (Calviño-Cancela 2002), promoviendo de esta forma la regeneración de las poblaciones de plantas, conectando la reproducción con el posterior reclutamiento de nuevos individuos (Godínez-Álvarez y col. 2002, Wang y Smith 2002, Calviño-Cancela y Martín-Herrero 2009).

Como resultado de la actividad de un dispersor, una semilla puede convertirse en una nueva planta adulta. Sin embargo, para que esto ocurra, es necesario que el dispersor contribuya efectivamente a la reproducción de la planta (Schupp 1993, Jordano y Schupp 2000, Godínez-Álvarez y col. 2002, Calviño-Cancela y Martín-Herrero 2009).

La efectividad de dispersión está definida como la contribución que un dispersor hace a la futura reproducción de la planta, la cual involucra dos componentes: (i) cuantitativo, que depende del número de visitas hechas por el dispersor a la planta, y el número de semillas dispersadas por visita, y (ii) cualitativo, que depende del paso de la semilla por el tracto digestivo del dispersor, y de la calidad del sitio donde la semilla es depositada, en términos de germinación y sobrevivencia (Schupp 1993). Por lo tanto, es importante evaluar ambos componentes de la efectividad, lo cual implica no sólo cuántas semillas son dispersadas, sino que también cuántos nuevos individuos podrán establecerse exitosamente (Schupp y col. 2010).

La germinación y el establecimiento son uno de los estados del ciclo de vida más críticos en el mantenimiento de las poblaciones de plantas (Harper 1977). Específicamente, muchas especies de cactus sólo pueden germinar y sobrevivir cuando no están expuestos a condiciones ambientales extremas como altos niveles de radiación y temperaturas elevadas del suelo, así como bajo contenido de humedad (Valiente-Banuet y Ezcurra 1991). El establecimiento de las plántulas bajo la fronda de otras especies de plantas, principalmente arbustos perennes, puede contrarrestar el efecto negativo impuesto por estas condiciones ambientales (Ellner y Shmida 1981, Callaway 1998). Muchas especies de cactus reclutan a través de facilitación (Turner y col. 1966), estableciendo relaciones específicas con otras especies de plantas bajo las cuales existe un microambiente favorable para la germinación, establecimiento, y subsecuente sobrevivencia de las plántulas (Turner y col. 1966, Franco y Nobel 1989, Mandujano y col. 1998). De esta forma, el proceso de facilitación (Callaway 1998, Godínez-Álvarez y col. 1999, Valiente-Banuet y Verdú 2007, Castillo y Valiente-Banuet 2010) enfatiza la

importancia de la dispersión de semillas dirigido hacia sitios específicos bajo la fronda de ciertas plantas que brindan protección a las plántulas, para lo cual los animales actúan como dispersores de semillas efectivos. Consecuentemente, un dispersor efectivo de semillas será aquel que disperse un gran número de semillas a estos sitios seguros lejos de las plantas parentales (Howe y Miriti 2004), contribuyendo a la futura reproducción de la planta (Schupp 1993), y un dispersor de semillas no-efectivo corresponderá a aquel que deposite las semillas bajo con-específicos, donde existe una mayor competencia denso-dependiente por los recursos con adultos ya establecidos, o donde semillas y/o plántulas tienen una mayor probabilidad de ser depredados (Janzen 1970, Connell 1971). Por lo tanto, es importante determinar las especies involucradas en el proceso de dispersión, que son capaces de depositar las semillas en sitios de reclutamiento exitoso donde éstas pueden sobrevivir (Nathan y Muller-Landau 2000, Schupp y col. 2010).

Contrario a lo anterior, la pérdida de dispersores de semillas puede gatillar la disrupción de esta interacción mutualista, reduciendo la regeneración de las especies de plantas (Wotton y Kelly 2011). Varios estudios han reportado la importancia de los frugívoros que actúan como dispersores de semillas para el mantenimiento de las poblaciones de plantas a nivel local, incluyendo los potenciales efectos de la disrupción de esta interacción (da Silva y Tabarelli 2000, Pejchar y col. 2008, Wotton y Kelly 2011, Liao y col. 2013). Tales impactos consideran una disminución en el reclutamiento, dada la pérdida del agente dispersor que lleva las semillas a los potenciales sitios de reclutamiento (Sethi y Howe 2009). Por lo tanto, evaluar el grado de dependencia entre animales y plantas es central para determinar los efectos que los dispersores de semillas tienen en el mantenimiento de las poblaciones naturales de plantas.

En este trabajo, se estudiarán los mecanismos de dispersión de frutos y semillas de dos especies de cactáceas columnares endémicas de Chile, *Leucostele chiloensis* (ex *Echinopsis chiloensis*) y *Eulychnia acida*, y los agentes bióticos involucrados en la dispersión, para determinar los factores involucrados en el mantenimiento de poblaciones locales de ambas especies. El estudio se realizó en la Reserva Nacional Las Chinchillas (31°30'S, 71°06'W, Illapel, Región de Coquimbo), ubicada a ~300 km al noreste de Santiago y a ~60 km al este de la costa del Pacífico. Específicamente, (i) se describirá el mecanismo de dispersión de los frutos de ambas especies, (ii) se determinará el ensamble de frugívoros asociados a ambas cactáceas, y (iii) se calculará la efectividad de dispersión de semillas de cada frugívoro asociado.

CAPÍTULO I

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FRUGIVORY IN *ECHINOPSIS CHILOENSIS*

Frugivory in *Echinopsis chiloensis* (Caryophyllales: Cactaceae)

Frugivoría en *Echinopsis chiloensis* (Caryophyllales: Cactaceae)

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Seed dispersal is a critical segment of the life cycle in plants. It involves fruit consumption and seed deposition on sites where environmental conditions are appropriate for germination and seedling establishment (Stoner & Henry 2008, Casado & Soriano 2010). Seed dispersal involves the action of mammals, birds, reptiles and insects, where seeds are often adhered to the body of animals or ingested and dispersed through defecation (Stoner & Henry 2008). Dispersal is a crucial process in semiarid environments as it provides seeds a chance to establish in safe sites. Although frugivory

is a widely studied mechanism in several types of environments, there is scarce information for arid and semiarid habitats (Jordano 2000). In this report we present data on the magnitude of frugivory by different consumer taxa on cactus fruits in a semiarid Chilean ecosystem.

Echinopsis chiloensis (Colla) Fried & Rowl is an endemic columnar cactus species widely distributed in north-central Chile that inhabits mainly equatorial-facing slopes in semiarid environments (Medel 2000, Cares et al. 2013). The blooming season of *E. chiloensis* extends from early September to mid-November, and the fruiting season from mid-October to late December or mid-January (Medel 2000). This species presents arborescent growth with basitonic structure, with more than one trunk near the base (Medel 2001). In spite of being a dominant species in semiarid environments, scarce information exists on its demography and growth. Hoffmann (1989) suggests that natural regeneration may be difficult and growth rate can be extremely low, which is consistent with previous findings from a three-year study that indicates young individuals height grow on average (\pm SE) 2.44 ± 0.4 cm year⁻¹ during years with average rainfall (Cares et al. 2013).

Currently, there is no published information about frugivory and seed dispersal of *E. chiloensis*. In this study, we report the results of field observations carried out during January of 2013 at the Reserva Nacional Las Chichillas (31°30'S, 71°06'W). This reserve is a protected area located ~60 km east from the Chilean Pacific coast. The climate of the study site is of a semiarid Mediterranean-type with most rainfall concentrated between June and August (di Castri & Hajek 1976). Mean annual

precipitation is 185.0 mm, with ample variation across years, alternating between long droughts and unusual years of high rainfall seemingly associated to El Niño events (di Castri & Hajek 1976, Jaksic 2001). The vegetation consists on thorny shrubs (Luebert & Pliscoff 2006) and columnar and spherical cactus species (Medel 2000, Medel et al. 2002, Hoffmann & Walter 2004).

In this study, we considered a species to be a fruit consumer when it ate, pecked or removed totally or partially the pulp of a cactus fruit. Feeding events were instances when an animal was observed performing at least one of the activities indicated above (Casado & Soriano 2010). Field observations indicate that fruits of *E. chiloensis* ripe and open on the cactus branch without drop by abscission (Figure 1A). To identify the bird species involved in frugivory, we performed observations early in the morning from 7:00 to 10:00, during 13 consecutive days (total sampling effort = 39 hours). Specifically, 142 cacti with at least one open fruit were scanned with binoculars (10 × 25). Only the Chilean mockingbird *Mimus thenca* (Molina 1782) was detected picking the fruits of *E. chiloensis* (total = 12 feeding events). Regarding ant species, preliminary observations revealed that ant activity was concentrated from 17:00 until dusk; therefore observations were carried out between 17:30 and 20:00 during 13 consecutive days (total sampling effort = 32.5 hours). On the average (\pm SE), 8.9 ± 1.6 cacti with open fruits/day were checked for ant presence, from which 2.1 ± 0.3 exhibited ants. Two ant species were recorded feeding on pulp and transporting seeds from the open fruits, *Conomyrma goetschi* (Goetsch & Menozzi 1935) (Fig. 1B) and *Solenopsis gayi* (Spinola 1851) (see also Medel & Vásquez 1994), with 19 and five feeding events, respectively. Even though fruits of *E. chiloensis* remain on the cactus branch after opening, two

mammal species, the rodent *Octodon degus* (Molina 1782) and the fox *Lycalopex culpaeus* (Molina 1782), were observed consuming fruits of this cactus species. It is likely that rodent species remove pulp and/or whole fruits directly from cactus branches by using horizontally oriented spines to climb, and foxes lick pulp of ripe fruits from low-heighted cactus individuals. Because these field records do not allow quantitative observations, wild rodent species were collected with folding wire mesh live-animal-traps (24 cm × 8 cm × 9 cm; FORMA: Products and Services, Santiago, Chile) baited with rolled oats and provided with cotton bedding to test for fruit consumption under captivity conditions. Overall, 300 traps per night were set during five days, and checked every morning. Captures included 46 *Phyllotis darwini* (Waterhouse 1837), 35 *O. degus*, 12 *Abrothrix olivaceus* (Waterhouse 1837) and two *Abrocoma bennetti* (Waterhouse 1837). At noon, all captured rodents were fed with ripe fruits of *E. chiloensis*. All the species tested consumed the fruits excepting *A. bennetti* that rejected consistently the offered fruit (percentage of effective feeding: *O. degus*: 24.5 %, *P. darwini*: 9.6 % and *A. olivaceus*: 4.3 %). Regarding fox species, evidence of fruit consumption by *L. culpaeus* based on the analysis of feces taken in different areas of the Reserve. A total of 48 complete fecal samples were collected, and 32 of them contained large amounts of seeds of *E. chiloensis* (mean ± SE: 18221 ± 2435 seeds per fecal sample). Additionally, it is worth to mention that *E. chiloensis* seeds were found in the stomach content of one individual of the marsupial *Thylamys elegans* (Waterhouse 1839), whose carcass was found in the study site, and dissected and analyzed in the laboratory.

In summary, field observations, no-choice feeding test and circumstantial evidence allowed identifying the fruit consumers of *E. chiloensis*, specifically during the peak time of the fruiting season (January). Frugivorous species included one bird species (*M. thenca*), four mammal species (*O. degus*, *P. darwini*, *A. olivaceus* and *L. culpaeus*), two ant species (*S. gayi* and *C. goetschi*), and one marsupial species (*T. elegans*). Although several bird species have been previously recorded in the study site (CONAF 1996), only *M. thenca* was observed consuming fruits of *E. chiloensis*. This result might be due to particular climatic conditions in the previous year, where the intense drought during 2012 translated into low bird diversity in the study site in the summer season of 2013. For this reason, we cannot rule out that other bird species belong the frugivorous guild of *E. chiloensis*. It is likely that repeated sampling across years complete the spectrum of bird species consuming fruits of *E. chiloensis*.

According to our field observations and no-choice feeding test, the frugivorous guild of *E. chiloensis* is diverse and not restricted to only one taxon. The fact that *E. chiloensis* depends on a generalized frugivorous assemblage for seed dispersal conveys a clear advantage for cactus recruitment. As birds, mammals, and ants have different patterns of habitat use, they provide a range of opportunities for seed dispersal and seedling establishment.

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CAPTION FOR FIGURES

Fig. 1: A) Ripe and dispersed fruits of *Echinopsis chiloensis* on the top of a cactus column. B) *Conomyrma goetschi* carrying a seed of *Echinopsis chiloensis*.

A) Fruto maduro y dispersado de *Echinopsis chiloensis* en la punta de una columna del cactus. B) *Conomyrma goetschi* transportando una semilla de *Echinopsis chiloensis*.

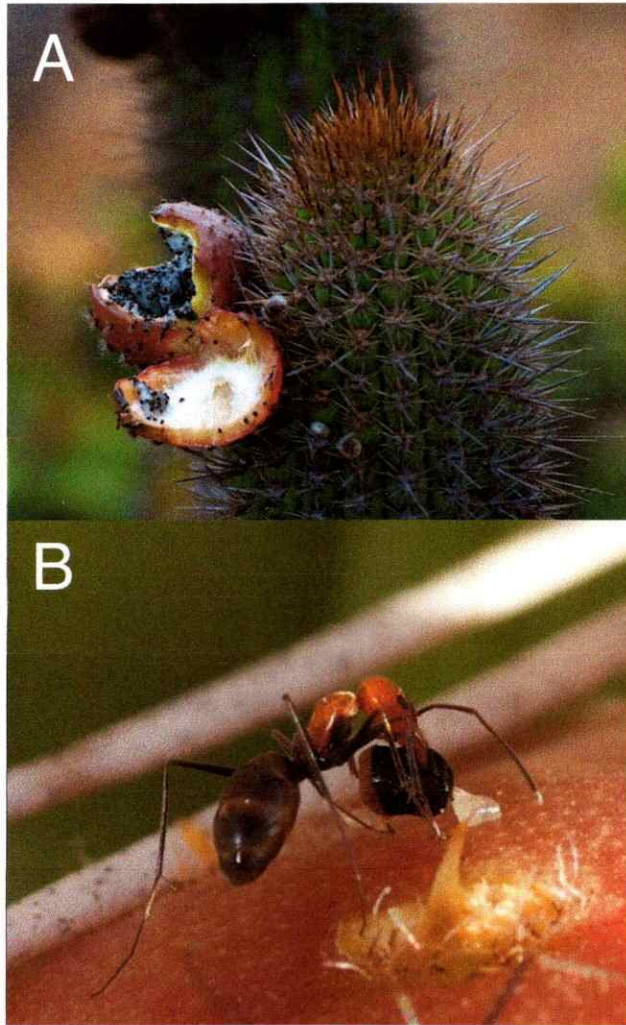


Fig. 1

CAPÍTULO II

Seed dispersal in the cactus *Leucostele chiloensis* (ex *Echinopsis chiloensis*): the bird *Mimus thenca*, the most effective disperser.

Abstract

Seed dispersal is an important ecological process because results in the recruitment and establishment of new individuals, through the interaction with frugivores that transport seeds to sites where the probability of seedling recruitment is high. In this study, carried out in the Reserva Nacional Las Chinchillas (31°30'S, 71°06'W), seed dispersal effectiveness was assessed for the columnar cactus *Leucostele chiloensis*, an endemic columnar cactus species widely distributed in north-central Chile. The dispersal effectiveness of different frugivores was determined, based on the quantity and quality components of seed dispersal. From all the frugivores recorded, the bird *Mimus thenca* acts as the main effective disperser, increasing the probability of germination and depositing seeds in safe sites for the seedling establishment. Other frugivores remove seeds from fruits carrying them to different places, but they deliver the seeds under conditions with low probability of recruitment. On the other hand, rodent species appear to be seed predators. The fact that mainly one effective disperser of *L. chiloensis* is important to understand both the pattern of occurrence of seedlings and recruitment limitations imposed by seed dispersal that determines the spatial distribution of this

cactus species.

Keywords:

Frugivores, seed dispersal, dispersal effectiveness, *Leucostele chiloensis*, *Mimus thenca*.

Introduction

Seed dispersal is an important ecological process that allows understanding the maintenance of plant populations through the interaction with animal vectors, which results in the recruitment and establishment of new individuals (Howe and Smallwood 1982; Willson and Traveset 2000; Godínez-Álvarez et al. 2002; Herrera 2002). Frugivores acting as effective seed dispersers play a fundamental role in the transportation of seeds from parental individuals to sites where the probability of seedling recruitment is high (Calviño-Cancela 2002), promoting plant renewal, connecting reproduction with later recruitment of new individuals, closing the loop for the natural regeneration of plant populations (Godínez-Álvarez et al. 2002; Wang and Smith 2002; Calviño-Cancela and Martín-Herrero 2009). As a result of disperser activity, a seed may become into a new adult plant, contributing to its effective reproduction (Schupp 1993). Therefore, it is important to assess the species involved in seed dispersal that are able to deposit the seeds in successful recruitment sites in which survival may occur (Nathan and Muller-Landau 2000; Schupp et al. 2010).

For example, germination and seedling establishment is one of the most critical stages of the life-cycle for the maintenance of viable populations (Harper 1977). Many species such as cacti only can recruit and survive when they are not exposed to extreme

environmental conditions such as high radiation levels and high soil temperatures as well as low moisture content (Valiente-Banuet and Ezcurra 1991). This situation can be reversed if the recruitment occurs through facilitation under the canopy of other plant species, which may counteract the negative effect imposed by desiccation and high soil temperatures (Ellner and Shmida 1981; Callaway 1998). Plant facilitation is a species-specific process (Callaway 1998; Castillo and Valiente-Banuet 2010) that emphasizes the importance of directed seed dispersal towards specific sites mostly beneath some plant species in order to be an effective seed disperser. Consequently, a effective seed disperser will be the one dispersing a large number of seeds to safe sites, contributing to the future reproduction of the plant (Schupp 1993), and a non-effective seed disperser would be a species able to deliver seeds under conspecifics where seedlings may be predated (Janzen 1970; Connell 1971), or where life-stage conflicts may occur (Schupp 1995; Deng et al. 2009).

In this study seed dispersal effectiveness was assessed for the columnar cactus *Leucostele chiloensis*, one of the most prominent endemic cactus species of Central Chile (Walter 2010). Young cacti of *L. chiloensis* recruit through facilitation mainly beneath the canopies of different plant species, but mostly beneath the shrub *Flourensia thurifera*, one of the most abundant native species in this semiarid environment (Cares et al. 2013a). We report seed disperser effectiveness based on the requirements of this cactus to germinate and establish (Schupp 1993). We assess the quantity component by identifying the frugivores involved in the seed dispersal and determining the number of seeds removed by each frugivorous species. In addition, we assess the quality component through the effect of seed ingestion and its implications on seed germination,

as well as the species that are able to deliver seeds beneath plant species that effectively enhance seedling establishment.

Materials and Methods

Natural history and study site

Leucostele chilensis is an endemic columnar cactus species widely distributed, inhabiting north-facing slopes in north-central Chile (Medel 2000) between the latitudes of 30°S and 36°S (Walter 2010). It presents arborescent growth with basitonic structure, being generally profusely branched or with several trunks emerging near the base (Medel 2001). Areoles of *L. chilensis* consist of 1-2 long central sclerified spines that project outward and 8-12 short lateral spines that point in all directions (Medel 2000). The blooming season extends from early September to mid-November, and the fruiting season from mid-October to late December or mid-January (Medel 2000). Fruits are green and grow on the cactus branch. Fruits are dehiscent and when they ripe, open on the branch without drop by abscission (Cares et al. 2013b).

Fieldwork was conducted in January 2013 in the Reserva Nacional Las Chinchillas (31°30'S, 71°06'W, Illapel, Coquimbo Region), a protected area located ~60 km east from the Chilean Pacific coast. The climate of the study site is semiarid Mediterranean-type with most rainfall concentrated between June and August (di Castri and Hajek 1976). Mean annual precipitation is 185.0 mm, with ample variation across years, alternating between long droughts and unusual years of high rainfall, seemingly associated to El Niño Southern Oscillation events (di Castri and Hajek 1976). The vegetation is characterized by thorny shrubs (Luebert and Pliscoff 2006), mainly

represented by the shrub species *F. thurifera*, *Bahia ambrosioides* and *Porlieria chilensis* (Medel et al. 2004), and the columnar cactus species *L. chiloensis* and *Eulychnia acida*, and the spherical cacti *Cumulopuntia sphaerica* and *Eriosyce aurata* (Hoffmann and Walter 2004; Medel et al. 2002; Cares et al. 2013a).

Frugivores

Focal observations were conducted to identify the frugivores as follows. Birds consuming fruits were recorded during the early morning hours. Ants carrying seeds of *L. chiloensis* were recorded from 17:00 until dusk, during the hours of more activity (Fuentes et al. 1996). Additionally, mammal species consuming fruits of this cactus species were recorded indirectly through faeces with seeds of *L. chiloensis* and preliminary field observations. Rodent species climb through branches by using horizontally oriented spines to reach the fruits, and foxes lick pulp of ripe fruits from low-heighted cactus individuals or consuming them on the ground (Cares et al. 2013b).

Quantity and quality components of birds, ants and mammals

Seed dispersal effectiveness was calculated according to Schupp (1993) by evaluating the different components (Fig. 1).

i) Quantity component. The frequency of visits of birds to *L. chiloensis* fruits was determined through daily focal observations on a hillside with 35 individuals (4.06 ± 0.9 (mean \pm SE) open fruits/cactus per day), which were marked with a paper plate and identified with a number in order to be scanned with binoculars (DOITE, LINCE 10 \times 25 model) from the slope in front (~150 m away). Observations were made early in the

morning from 7:00 to 10:00, during 13 consecutive days (total sampling effort = 39 hours). Visitor species, frequency and number of pecks of each bird on fruits were recorded. Additionally, faeces of birds containing seeds of *L. chilensis* were also collected in order to remove seeds for germination experiments.

Observations of ants were carried out between 17:30 and 20:00 during 13 consecutive days (total sampling effort = 32.5 hours). Cactus individuals were monitored randomly for the presence of ants (8.89 ± 1.57 (mean \pm SE) cacti/day). The number of ants was checked per unit time (10 minutes), by counting all ants going down from the cactus branch with seeds, pulp or nothingness, for a total of 33 focal cacti. The number of seeds removed was quantified as total number of seeds transported by ants during 5.5 hours.

Regarding mammals, rodent individuals were collected with folding wire mesh live animal-traps (24 cm \times 8 cm \times 9 cm; FORMA: Products and Services, Santiago, Chile) baited with rolled oats and provided with cotton bedding, to perform no-choice feeding test under captivity conditions. Overall, 94 rodents were fed with a fruit of *L. chilensis*, and its faeces were collected after 24 hours. To examine if the fox species inhabiting the Reserve was consuming fruits of *L. chilensis*, all faeces of foxes found in the study site ($n = 48$) were individually collected in paper bags and analyzed later, in order to determine the number of seeds per faeces.

The total number of seeds removed by birds was obtained by estimating the average number of seeds consumed per visit (estimated as the number of seeds per peck multiplied by the number of pecks) multiplied by the average of visits/day, and calculated for all fruiting season. The number of seeds per peck was estimated from the

number of seeds contained in the volume of the beak. For ant species, the total number of seeds removed was calculated by the average number of seeds removed per unit of time multiplied by the average of visits/day, and calculated for all fruiting season (ca. 30 days for 2013 season). The seeds removed by rodents and the fox species were estimated as the number of living seeds extracted directly from faeces collected after no-choice feeding test for rodents, and the sum of all seeds found in the fox faeces ($n = 32$).

Relative abundance of birds in the study site was obtained from Martínez del Río et al. (1995). The number of seeds removed by foxes was estimated as a total number of faeces found in the study area ($n = 48$) per kilometer-walked as an approach of relative abundance (Aranda 2000). Ant removal was calculated as the total number of ants going down from a specific cactus branch per unit of time. Relative abundance of rodents was obtained from a sampling carried out in the study site in the 2013 season (Botto-Mahan, unpublished data).

ii) Quality component. Germination experiments were performed to determine the proportion of germinated seeds obtained from faeces collected for the frugivores (i.e., birds, fox and rodents) compared with seeds obtained from fresh fruits used as control treatment. For each treatment (three different species and one control), seeds were sown in plastic pots with gravel as a substrate, moistened with filtered water and placed in a growth chamber (PITEC, BIOREF-38 model) at 25°C with a 14:10 h (day/night) photoperiod. Germination was recorded daily for 42 days, or until no germinating seeds were observed for more than seven days. The criterion used to consider a seed germinated was radicle emergence. The number of seeds sown per pot was 30 for all treatment except for the rodent, varying among one and 30 seeds, depending on the

defecated seeds available. The number of pots also varied among nine and 32 per treatment, depending on the number of faeces collected (one pot per faeces). To assess the differences in the effect of gut passage on seeds among frugivores, germination was examined with generalized linear models (GLM) using a logit link and binomial distribution (Crawley 2007). Null hypothesis considered an equal number of germinated seeds among the treatments and control.

Seed germination was calculated as a proportion of seeds germinated with respect to total seeds sown in the pots for all treatments excepting rodents, which act as seed predators since very few viable seeds remain in their faeces. Then, for rodents, seed germination was estimated as a proportion of seeds germinated with respect to total seeds eaten in the no-choice feeding tests.

To estimate the probability of depositing seeds under shrubs for the bird species, the number of visits of birds to different perching shrubs, bare soil, and the two most abundant columnar cactus species (*L. chiloensis* and *E. acida*) was extracted from Rivera-Hutinel (2008), whereby was estimated a perching proportion in each microsite. This proportion was used as an estimator of the probability to deposit seeds on that microsite. The probability of depositing seeds by frugivorous species in different sites (under shrubs or bare soil) was extracted from Cares et al. (2013a).

Seed dispersal effectiveness calculations

Effectiveness of each frugivore species was calculated as the product of the four subcomponents (Fig. 1): number of seeds dispersed \times relative abundance of frugivore \times proportion of seed germination after gut passage \times deposition probability under shrubs

(Godínez-Álvarez et al. 2002).

Results

Frugivores

Seven species were identified as fruit consumers of *L. chilensis*: the Chilean mockingbird, *Mimus thenca* (Mimidae), two ant species, *Solenopsis gayi* and *Conomyrma goetschi* (Formicidae), the Culpeo fox, *Lycalopex culpaeus* (Canidae). Additionally, four small mammal species were captured and submitted to no-choice feeding tests, the Brush-tailed rat *Octodon degus* (Octodontidae), the Leaf-eared mouse *Phyllotis darwini* (Muridae), the Forest-dwelling mouse *Abrothrix olivaceus* (Cricetidae) and the Chinchilla rat *Abrocoma bennetti* (Abrocomidae) The latter was the only rodent species that under captivity condition did not eat fruits of *L. chilensis*.

Effect of gut passage

Seeds defecated by *M. thenca* presented the highest germination with a proportion of 0.91, differing significantly from control seeds (0.84), followed for *L. culpaeus* (0.89), which also differed significantly from control treatment (Table 1). Few seeds could be rescued from faeces of *O. degus* because most were destroyed. The remaining seeds defecated (less than 0.01%) by this rodent showed less than 0.1 germination proportion, indicating that this mouse is a seed predator. No living seeds were found in *P. darwini* and *A. olivaceus* faeces, indicating that in this system rodent species act mainly as seed predators. The estimated germination rates for *M. thenca* and *L. culpaeus* were (mean \pm SE) 0.59 ± 0.01 and 0.58 ± 0.02 seeds/day, respectively. The estimated germination rates

for *O. degus* was (mean \pm SE) 0.13 ± 0.05 seeds/day, the lowest due to the low number of seeds found in their faeces.

Effectiveness of seed dispersal

The dispersal effectiveness estimated for these species showed that *M. thenca* and *L. culpaeus* were effective dispersers for *L. chiloensis*, however, *L. culpaeus* was less efficient depositing seeds in sites with higher probability of germination and recruitment of *L. chiloensis* than *M. thenca*, which has a higher probability of seed deposition under *F. thurifera* (Table 2). Approximately 50% of seeds removed by *M. thenca* are deposited beneath *F. thurifera*, acting as the most important nurse plant for *L. chiloensis* (Cares et al. 2013a). Regarding ant species, the fate of the removed seeds was not observed in the field, therefore, seed dispersal effectiveness could not be calculated. At last, the rodent species *P. darwini* and *A. olivaceus* destroyed seeds through gut passage, but few alive seeds could be extracted from faeces of *O. degus*, not discarding it as seed disperser.

Discussion

The main finding of this study is that the fruits of *L. chiloensis* are consumed by a total of seven frugivores, which results in a low number of species interacting with this cactus compared with other cactus species. In the Tehuacán Valley, México, Godínez-Álvarez et al. (2002) described at least seven birds and four bat species consuming the fruits of *Neubuxbaumia tetetzo*, and fifty bird species are described for *Opuntia rastrera* in the Chihuahuan Desert (Montiel and Montaña 2000). In other plant species, several frugivorous species also are reported, for example, Jordano and Schupp (2000) found

about 26 bird species consuming fruits of *Prunus mahaleb* in southeastern Spain, and at least three effective dispersers are described for *Corema album* in northwest Spain (Calviño-Cancela and Martín-Herrero 2009). For *L. chiloensis*, *M. thenca* and *L. culpaeus* could act as effective seed disperser, but only the first deposits the seeds beneath the most important nurse shrub species, able to generate suitable conditions for seedling establishment and survivorship (Cares et al. 2013a). On the other hand, *L. culpaeus* deposits a large amount of seeds in open sites (i.e., a more stressful habitat), and probably this canid is the responsible, at least in part, of the recruitment in this microhabitat. Furthermore, no regeneration has been observed under conspecifics of *L. chiloensis* (Cares et al. 2013a); therefore, this cactus species largely depends on movement of seeds by animal dispersers to most suitable habitats for plant recruitment, providing escape from high density of competing siblings and away from potential predators near parents (Howe and Smallwood 1982).

Rodent species appear to be seed predators (Janzen 1971), since seeds in faeces of *P. darwini* and *A. olivaceus* were destroyed, and a few seeds could be rescued from *O. degus* faeces, representing a low percentage of germination compared to the number of ingested seeds. Nevertheless, seeds dispersed by *O. degus* could potentially germinate in suitable microhabitats in the field; therefore, this species is not completely excluded as seed disperser. Ant species in Chile are generalist in the use of resources and not granivore specialists in the occupation of seeds (Medel and Vásquez 1994; Fuentes et al. 1996). Even though it has been reported previously that ants could play an important role as primary cactus seed dispersers (Munguía-Rosas et al. 2009), at least in this semiarid system, the role of ants requires future observations (see Medel and Vásquez

1994; Medel and Fuentes 1995), because the effect of ants on seeds (by the seed cleaning process), seed fate after removal and seedling establishment success are unknown.

Due to their requirements for germination and establishment, *L. chiloensis* occurs heterogeneously in the environment, most of them randomly distributed under the canopy of nurse plants (Cares et al. 2013a). The process of seed dispersal may indirectly affect the probability of dispersal to suitable sites, and it acts as a determining factor of seed-seedling conflicts (Schupp 1995). The finding that *M. thenca* is dispersing effectively the seeds of *L. chiloensis* is essential to understand the pattern of occurrence of seedlings and recruitment limitations both imposed by seed dispersal that determines the spatial distribution of this cactus species (Drezner 2006).

The fact that almost one effective disperser of *L. chiloensis* is observed suggests that a long-term effect of frugivore diversity loss could be taking place. Previous studies have documented the effect of dispersal failure as result of a reduction in the number of frugivores (Bond and Slingsby 1984; Bond 1994; Bleher and Böhning-Gaese 2001; Wang and Smith 2002; Farwig and Berens 2012), which can affect plant population dynamics, especially if the species are recruitment limited. Even though *L. chiloensis* presents regeneration at a local scale, this process may affect population dynamics at larger scale. Wotton and Kelly (2011) report the dependence of seedling recruitment and the impact in dispersal failure in two temperate-zone large-seeded New Zealand trees that largely depend on a single frugivore, highlighting the importance of mutualistic interactions in the local regeneration of plant populations. The contribution of seed dispersers to *L. chiloensis* is important for maintenance of the population, providing a

greater probability of survival to the seedlings, and increasing the range of spread for this cactus species. The disruption of this interaction could lead to a reduction of the reproductive success and an expansion range limitation, and consequently, a potential threat of local extinction (Traveset and Riera 2005).

In brief, this study shows that exists a high dependence of *L. chilensis* by a single effective disperser, the bird *M. thenca*, which could involve potential serious risks for the maintenance of local populations of this cactus species in the near future.

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Caption for figure

Fig. 1. Hierarchical flow chart representing the components of seed dispersal effectiveness (SDE) (modified from Schupp et al. 2010).

Tables

Table 1. Results from GLM for the effect of passage through the gut of frugivores on germination of seeds of *L. chiloensis*. All treatments are compared with control seeds ($n = 9$), and n indicates number of replicates (each replicate corresponds to a pot sown with seeds from the same faeces).

	Estimate	SE	<i>P</i>
<i>Lycalopex culpaeus</i> ($n = 32$)	0.45	0.19	0.02
<i>Mimus thenca</i> ($n = 9$)	0.92	0.29	0.001
<i>Octodon degus</i> ($n = 12$)	0.44	0.39	0.25

Table 2. Dispersal effectiveness for different frugivores of *L. chilensis*.

¹Relative abundance of individuals estimated according to the sources described in Materials and Methods.

²Proportion of seeds germinating after gut passage of frugivorous species.

³Number in parentheses indicates the proportion of seeds that *M. thenca* dispersed in each microsite.

⁴ Effectiveness = number of seed dispersed \times relative abundance \times handling \times deposition probability under shrubs. Number in parentheses indicates the proportion of seeds that become adults respect the number of seed dispersed.

Species	Quantity component		Handling ²	Quality component			Effectiveness ⁴		
	Number of seed dispersed	Relative Abundance ¹		<i>E. acida</i>	<i>L. chilensis</i>	Shrubs	Open sites	Shrubs	Open sites
<i>Mimus thenca</i>	359.1	0.6	0.91	0.00 (0.12)	0.00 (0.18)	0.60 (0.56)	0.40 (0.12)	117.64 (0.32)	78.43 (0.21)
<i>Lycalopex culpaeus</i>	583092	0.4	0.89	0.00	0.00	0.00	0.40 (1.0)	0.00	83032.3 (0.14)

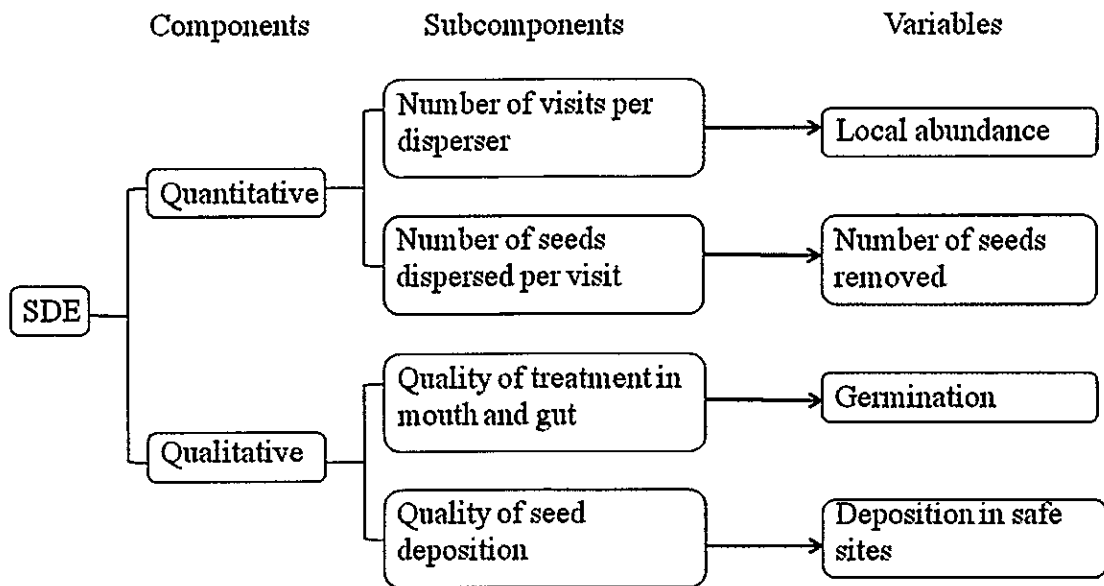
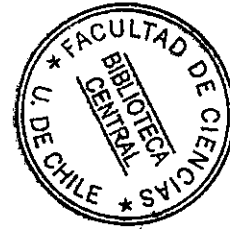


Fig. 1.

CAPÍTULO III



Mechanism of fruit dispersal in *Eulychnia acida*: evidence of a megafaunal dispersal syndrome?

Frugivore loss worldwide is increasing in nowadays communities representing a serious threat for plant persistence when the interaction with animal dispersers is essential for plant reproduction (Corlett 2007). Consequently, unraveling the degree of dependence between animal-plant mutualism is central for conservation biologist, in order to determine the effects of the loss of partners on plant reproductive failure, and risk of extinction (Bond 1994). For example, several studies have reported the importance of seed dispersers, mainly larger-bodied vertebrates, for the maintenance of local plant populations, including the potential impacts on the disruption of this interaction (Pejchar et al. 2008, Wotton and Kelly 2011, Liao et al. 2013). Such impacts consider a decrease in the seedlings recruitment, once the loss of dispersal agents that carry the seeds at potential recruitment sites occurs (Sethi and Howe 2009). In fact, plant species risk of extinction at regional scale also may occur through the disruption of seed dispersal (da Silva and Tabarelli 2000). However, in sites where frugivores have declined, introduced large herbivorous vertebrates as surrogate dispersal agents have replaced seed dispersers (Janzen 1982). Janzen (1986) shows that introduced livestock could have replaced in some extent extinct herbivores that probably ate fruits and dispersed seeds in Nopaleras,

a vegetation type dominated by different species of *Opuntia*, in the Chihuahuan Desert of Mexico. Moreover, the importance of ungulates as agent of plant dissemination (Pakeman et al. 2002, Couvreur et al. 2004) indicates that goats can effectively disperse viable seeds of diverse species of cactus (Baraza and Valiente 2008). Presumed absence of mammalian vertebrates that acted as seed disperser, such as extinct horses, gomphotheres and ground sloths, in sites where there are plants with fruits exhibiting traits that now are mostly anachronism, could explain in part the mutualist interaction with present-day domestic animals (Guimaraes et al. 2008). Janzen and Martin (1982) proposed that seed dispersal by extinct megafauna is central to understand certain plant reproductive traits in Central America lowland forest, suggesting that some fruits may even be “megafaunal anachronisms”, a dispersal syndrome that best explains the features of the fruits by interactions with extinct animals.

Eulychnia acida is an endemic columnar cactus species that inhabits north-facing slopes in semiarid Chile (Medel 2000, Cares et al. 2013), and widely distributed in the Coquimbo Region (29°54'S, 71°15'W), from sea level to 1200 m.a.s.l. (Masson et al. 2011). This cactus species presents a branched arborescent growth, from 1.5 to 4.0 m of height, usually with only one trunk (Hoffmann 1989). The blooming season extends from early September to mid-November, and the fruiting season from mid-October to late December or mid-January (Medel, 2000). Scarce information has been reported about the growth of columnar cacti, but Hoffmann (1989) suggests that natural regeneration may be difficult and growth rate extremely low. In fact, in a protected area of semiarid Chile only 56 young cacti of *E. acida* (less than 30 cm height) were recorded in approximately 3 ha, with at least 296 adult individuals in the same area (RA Cares

and R Medel, unpublished data), suggesting a low recruitment and scarce regeneration (i.e., demographic bottleneck). Additionally, a previous report indicates that young individual growth of *E. acida* is very low, on average (\pm SE) 6.7 ± 0.7 cm height in a period of three years with average rainfall (Cares et al. 2013).

Concerning frugivory and seed dispersal, *E. acida* fruits exhibit features that allow hypothesizing evidence of megafaunal dispersal syndrome according to Janzen and Martin (1982), which may account for its demographic bottleneck. Some evidences include that: (i) the fruits are indehiscent, therefore, seeds cannot be dispersed abiotically, (ii) all fruits fall down from the cactus upon ripening, (iii) fruits are larger than the potential native frugivores that could eat them, (iv) there is a high proportion of fruit crop on the ground not consumed by any potential dispersal agent, (v) small native rodents that usually act as seed predators, may be the only dispersal agent, and (vi) the fallen fruits are occasionally eaten by introduced large herbivores such as modern horses, cattle, donkeys and goats, and seeds that pass through the gut of these animals could potentially germinate.

Field observations were carried out during February of 2013 in the Reserva Nacional Las Chichillas (31°30'S, 71°06'W), to identify frugivores and seed dispersers of *E. acida*. This reserve is a protected area located ~60 km east from the Chilean Pacific coast. The climate of the study site is of a semiarid Mediterranean-type with most rainfall concentrated between June and August (di Castri and Hajek 1976). Mean annual precipitation is 185.0 mm, with ample variation across years, alternating between long droughts and unusual years of high rainfall seemingly associated to El Niño events (di Castri and Hajek 1976, Jaksic 2001). The vegetation consists on thorny shrubs (Luebert

and Pliscoff 2006) and columnar and spherical cactus species (Medel 2000, Medel et al. 2002, Hoffmann and Walter 2004).

In this study, to identify the species involved in *E. acida* fruit consumption, fifty 1 × 1 m footprint traps were established on the hills, where fresh fruits were found on the ground. In the middle of each footprint trap one fruit was placed as bait (mean fruit size ± SE: 49.42 ± 4.78 mm width, 48.46 ± 3.94 mm length, n = 50), and tied with a nylon thread to keep track of fruit and seed consumers. Traps were checked for animal tracks during six consecutive days. Footprints were recorded with a digital camera along with a tape measure. If the fruit had not been consumed, the footprint trap was brushed again and the fruit was left in the same place. Overall, three footprints were identified, corresponding to two bird species, the Chilean tinamou *Nothoprocta perdicaria* (n = 19) and the Chilean mockingbird *Mimus thenca* (n = 15), and one small mammal species, the brush-tailed rat *Octodon degus* (n = 11). Nevertheless, only *O. degus* ate the fruit completely. In the latter case, fruits were not in the trap, instead they had been brought by *O. degus* to their caves and only the remnants of the eaten fruit at the end of the nylon thread were recovered (n = 8). About the two bird species, only *N. perdicaria* is suggested as a potential fruit consumer, because the fruit was found with signs of having been pecked (n = 6), but not enough to swallow seeds. On the other hand, *M. thenca* only pecked the fruit once; therefore, the evidence of fruit intake is insufficient.

In order to perform no-choice feeding test to support our field records, individuals of *O. degus* were collected with folding wire mesh live animal-traps (24 cm × 8 cm × 9 cm; FORMA: Products and Services, Santiago, Chile) baited with rolled oats and provided with cotton bedding to test for fruit consumption under captivity

conditions. Overall, 150 traps per night were set during five consecutive days, between 19:00 and 09:00 hrs, and checked every morning. Individuals of *O. degus* captured ($n = 33$) were fed with ripe fruits of *E. acida*, and after three days, their faeces were collected from their cages to look for seeds. All individuals consumed the whole fruits, but it was only possible to recover one or two seeds per faeces. Due to this finding, it is suggested that this rodent species destroys and kills most seeds passing through their digestive tracts.

Germination experiments were performed to determine the proportion of germinated seeds obtained from faeces and from fresh fruits (control treatment). Seeds were sown in plastic pots with gravel as a substrate, moistened with filtered water and placed in growth chamber (PITEC, BIOREF-38 model) at 25°C with a 14:10 h (day/night) photoperiod. Germination was recorded daily for 42 days, or until no germinating seeds were observed for more than seven days. The criterion used to consider a seed germinated was radicle emergence. The number of seeds sown per pots was two for control treatment ($n = 15$ pots) and among one and three seeds for the rodent ($n = 9$ pots), depending on the availability of defecated seeds. To assess the differences in the effect of gut passage on seeds between *O. degus* and control, germination was examined with generalized linear models (GLM) using a logit link and binomial distribution (Crawley 2007). Null hypothesis considered an equal number of germinated seeds between the treatments. Seeds defecated by *O. degus* presented a germination percentage of 20% not differing significantly from controls with 13.3% (Estimate = -0.37, SE = 0.77, $p = 0.62$). The estimated germination rates for *O. degus* and control were (mean \pm SE) 0.008 ± 0.004 and 0.02 ± 0.008 seeds/day, respectively.

In this study, there were not found frugivores associated to seed dispersal of *E. acida*, because neither species carried seeds to sites with higher probability of recruitment, nor increased the probability of germination. This suggests that the current fruit dispersal mechanism of this cactus species could be accounting in some extent of a megafaunal dispersal syndrome, because features of *E. acida* fruits coincide with those for plants with megafaunal dispersal syndrome according to Janzen and Martin (1982). Alternatively, fleshy fruits of *E. acida* might have evolved as a plant adaptation for seed defense from animals present in the past, rather than a coevolutionary process of plant-disperser mutualism (Mack 2000).

Currently, populations of *E. acida* in the Reserva Nacional Las Chinchillas have a low recruitment compared with other endemic columnar cactus species in the same study site, *Leucostele chiloensis* (Cares et al. 2013), and presents very low rate of regeneration within the Reserve (R. Medel, unpublished data). This could be the consequence of the frugivore loss, which could have corresponded to South American late Pleistocene megafauna that became extinct at the end of the period (Marshall 1981), and which has not been replaced for present-day domestic animals such as livestock and cattle, for example. However, it has been observed donkeys (*Equus africanus asinus*) and goats (*Capra aegagrus hircus*), and also guanacos (*Lama guanicoe*) in other sites along *E. acida* distribution range eating their fruits (P. Guerrero, personal communication). It is possible that these mammal species are acting as seed dispersers outside the Reserve, and therefore, a greater regeneration is occurring in these areas. Additionally, it is worth considering the exploitation of *E. acida* fruits for human consumption (Salvatierra et al. 2010), which also results in the maintenance of

populations of this cactus species outside of conservation sites, but may cause profound changes in seed dispersal patterns of unmanaged populations (Guimaraes 2008).

There is scarce information on the effects of recently extinct large herbivores on vegetation, probably because it has been difficult to elucidate whether the megafaunal extinctions had a human or environmental cause (Johnson 2009). However, there is no doubt that plants with megafaunal dispersal syndrome, in sites where their seed dispersers are now extinct, could be suffering declines in distribution range and genetic pool, potentially leading to extinction. It is necessary to understand the ecological functions of contemporary plant communities in the ecosystems, considering the disrupted interactions with extinct megafauna, for the management and conservation of plant species exhibiting anachronistic fruits.

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CONCLUSIONES

De los resultados de esta tesis emergen las siguientes conclusiones generales:

1. *Leucostele chiloensis* y *Eulychnia acida* presentan diferentes mecanismos de dispersión de frutos. Mientras que el fruto dehiscente de *L. chiloensis* abre cuando madura, aún pegado al brazo del cactus, el fruto indehiscente de *E. acida* cae por abscisión. Dadas estas diferencias, los mecanismos de dispersión de semillas son distintos.
2. Los frutos de *L. chiloensis* son consumidos por siete frugívoros, el ave *Mimus thenca*, dos especies de hormigas, *Solenopsis gayi* y *Conomyrma goetschi*, el zorro culpeo *Lycalopex culpaeus*, y tres especies de roedores, *Octodon degus*, *Phyllotis darwini* y *Abrothrix olivaceus*. Se informa la presencia de semillas de esta cactácea en el tracto digestivo de un ejemplar del marsupial *Thylamys elegans*. Este resultado indica un bajo número de especies frugívoras interactuando con *L. chiloensis* en este sistema semiárido de Chile.
3. *M. thenca* y *L. culpaeus* actúan como dispersores de semillas de *L. chiloensis*, ya que ambos aumentan significativamente la germinación. Sin embargo, *L. culpaeus* es un dispersor menos eficiente debido a que deposita las semillas en sitios abiertos donde el reclutamiento de *L. chiloensis* es menor. *M. thenca* deposita las semillas en sitios donde

existe mayor probabilidad de germinación y establecimiento. Ambos podrían estar dando cuenta en distinta medida del reclutamiento de *L. chilensis*.

4. Los roedores *P. darwini* y *A. olivaceus* son identificados como depredadores de semillas, dado que destruyen las semillas al pasar por su tracto digestivo. No se descarta a *O. degus* como dispersor de semillas.

5. Las interacciones mutualistas entre *L. chilensis* y los dispersores encontrados son importantes para el éxito en la reproducción de esta especie de cactus. La disrupción de estas interacciones podría llevar a una reducción en el éxito reproductivo y a limitar su rango de expansión, llevando a poblaciones de *L. chilensis* a potenciales amenazas de extinción local.

6. En *E. acida*, sólo *O. degus* fue detectado como consumidor de frutos. Sin embargo, este roedor destruye la mayoría de las semillas al pasar por su tracto digestivo, por lo que es considerado principalmente como un depredador de semillas.

7. Varias características del fruto de *E. acida* concuerdan con la descripción de frutos con síndrome de dispersión por megafauna. Esta evidencia y la ausencia de dispersores de semillas en el sitio de estudio en la actualidad, sugieren que el mecanismo de dispersión de frutos de *E. acida* observado podría dar cuenta, en alguna medida, de este síndrome. Se sugiere que los frutos de *E. acida* podrían dar cuenta de un rasgo anacrónico.

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