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Frugivory and seed dispersal in the endemic cactus *Eulychnia acida*: extending the anachronism hypothesis to the Chilean Mediterranean ecosystem

Rocío A. Cares[1†], Consuelo Sáez-Cordovez[1†], Alfonso Valiente-Banuet[2], Rodrigo Medel[1*] and Carezza Botto-Mahan[1]

Abstract

Background: *Eulychnia acida* is an endemic Chilean cactus species whose fruits show several traits that, taken as a whole, are compatible with a seed dispersal syndrome by large herbivore vertebrates. Since only a few large native mammals exist in Chile at present, cactus fruit consumption and seed dispersal may be coopted by introduced mammals as predicted by Janzen and Martin's (1982) hypothesis for tropical ecosystems.

Findings: We describe the current frugivore species of *E. acida* in a protected semiarid-Mediterranean ecosystem using field measurements and feeding experiments. In addition, to examine a potential role as seed dispersers of the cactus species, we offered fruits and performed germination tests on seeds defecated by *Lama guanicoe* and the introduced goat *Capra a. hircus* under captivity conditions. Our data indicate that while fruits of *E. acida* are pecked by the Chilean tinamou, *Nothoprocta perdicaria*, and the Chilean mockingbird, *Mimus thenca*, and eaten by the brush-tailed rodent, *Octodon degus*, none of these species could be considered a legitimate seed disperser. Unlike *L. guanicoe*, the goat *C. a. hircus* did not reduce seed germination, having a neutral effect.

Conclusions: Results from this study indicate that introduced *C. a. hircus* was the only species showing a potential role in the seed dispersal process of *E. acida*. In the absence of native frugivore species, goats might play an important role in population recruitment of the endemic cactus. These results extend Janzen and Martin's (1982) anachronism hypothesis to the Chilean Mediterranean ecosystem.

Keywords: *Eulychnia acida*, Seed dispersal, Frugivory, Seeds, Goats, *Lama guanicoe*, *Octodon degus*, Anachronism

Background

Frugivory and seed dispersal are key ecological processes involved in the demography and maintenance of plant populations [1–4]. Frugivore species play a fundamental role in seed dispersal, as they increase the probability of seed germination by removing the pulp and/or through gut passage and carry seeds away from parental individuals to sites where the probability of seedling recruitment may be higher [5, 6]. It has been long accepted that current associations between plant and frugivore species are the outcome of selective forces that fit suites of fruit features to those animal species which maximize the seed dispersal process and plant recruitment [7, 8]. Nevertheless, in some circumstances, fruits may exhibit morphological traits best explained as adaptations for seed dispersal by extinct animal species, a phenomenon referred as "seed dispersal anachronism". Guimaraes et al. [9] indicated that some current Neotropical fruits exhibit features that do not fit to dispersers present today but seem to exhibit apparent adaptations for the dispersal by large animals which are now extinct. Janzen and Martin [10] hypothesized that introduced and large herbivore vertebrates may act as surrogate dispersal

* Correspondence: rmedel@uchile.cl
†Rocío A. Cares and Consuelo Sáez-Cordovez contributed equally to this work.
[1]Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Ñuñoa, Santiago, Chile
Full list of author information is available at the end of the article

agents in places where native frugivorous have disappeared. While in tropical forests some fleshy fruits show putative adaptations to animals that are extinct nowadays [9–11], this kind of study is lacking in Mediterranean ecosystems. This omission is unfortunate, as extinction of large herbivore mammals putatively involved in seed dispersal may be not only restricted to tropical ecosystems but encompass most Neotropical ones [10], including the current Chilean Mediterranean ecosystem.

Eulychnia acida (Cactaceae) is an endemic columnar cactus species that inhabits north-facing slopes in semiarid Chile [12] (Fig. 1). Its geographic distribution ranges from Atacama to the Coquimbo Region (27°22' S, 70° 19' W to 29° 57' S, 71° 20' W; Fig. 2) [13]. The fruit is spherical, large and indehiscent (5–6 cm in diameter) (Fig. 1), with a yellowish-green color and covered with small scales [14]. Each fruit contains on average (±SE) 1930 (±95.7) small black seeds embedded in a white sour pulp ($n = 315$; R. Medel, unpublished data). The fruiting season of *E. acida* ranges from mid-October to early-January [15]. When ripe, fruits fall from the cactus branch, which often results in a high proportion of the fruit crop lying on the ground. No native species has been hitherto reported to remove or eat them. However, in unprotected semiarid-Mediterranean areas, individuals of *Capra a. hircus* (goats) have been observed consuming *E. acida* fruits (R. Cares, personal observation), which is consistent with studies highlighting the role of goats as seed dispersers of cactus species in other latitudes. For example, Baraza and Valiente-Banuet [16] found that seeds of the endemic cactus species *Echinocactus platyacanthus* and *Ferocactus robustus* recovered from goat feces had high germination capacity. Baraza and Fernández-Osores [17] reported that goats disperse the seeds of two additional cactus species, *Ferocactus flavovirens* and *Ferocactus latispinus*. In Chile, a potential large-sized fruit consumer and disperser of *E. acida* is the native camelid *Lama guanicoe* (guanaco), which is sometimes observed in the foothills of the Andes Mountain Range in north-central Chile. It is likely that *L. guanicoe* reached high population numbers in places where nowadays it is locally extinct [18]. In the arid coast of the Atacama Desert, *L. guanicoe* eats mostly lichens and succulent plants, such as *Eulychnia iquiquensis* [19], which suggests a role in the seed dispersal process of cactus species.

The first goal of this study was to describe the native species eating the fruits and dispersing the seeds of *E. acida*. To this end, we carried out fruit-consuming field experiments in a protected area (Las Chinchillas National Reserve) and performed laboratory germination

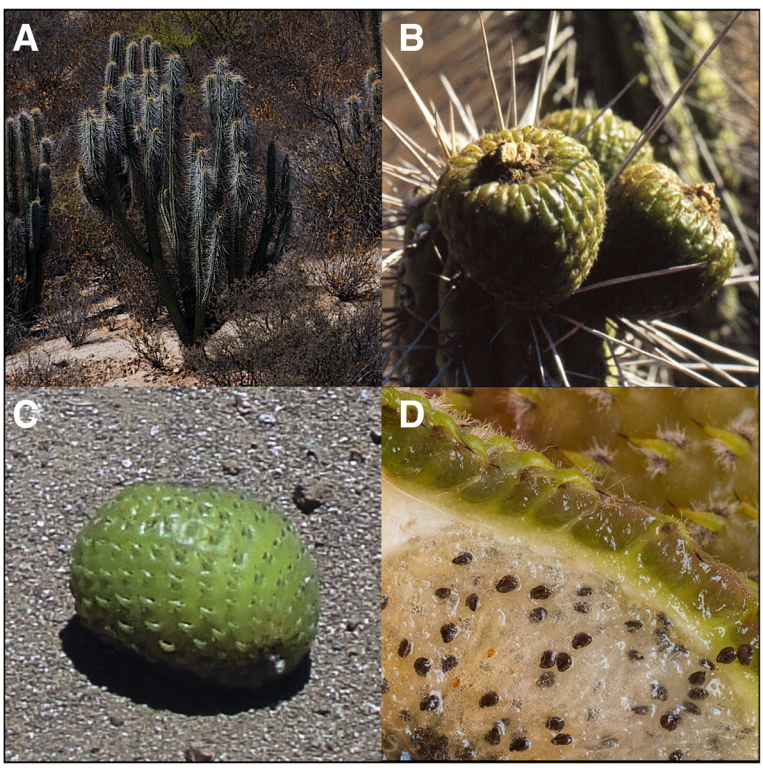

Fig. 1 Adult specimen of *Eulychnia acida* (**a**), *Eulychnia acida* fruit adhered to the stem of cactus (**b**), *Eulychnia acida* fruit after being naturally excised (**c**), and pulp of *Eulychnia acida* fruit (**d**). Pulp photograph by José Cañas

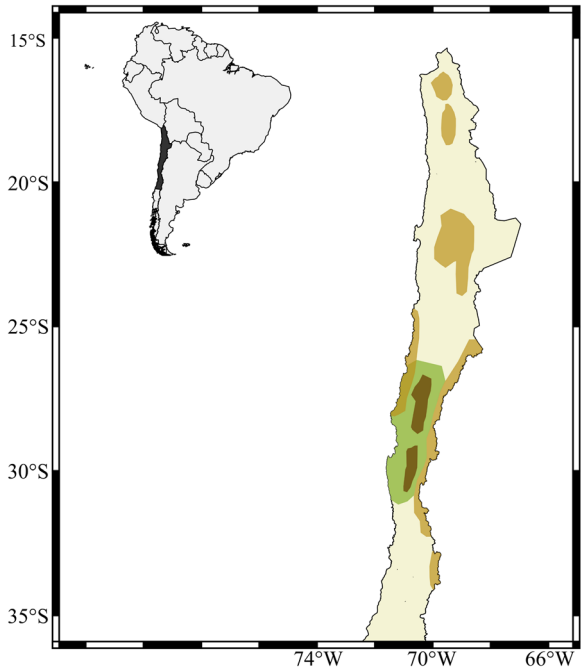

Fig. 2 Map of Chile depicting the distribution of *Eulychnia acida* (green color), guanaco (light brown color) and goat (dark brown color)

experiments. Our second goal was to evaluate whether seed passage through guanaco and goat digestive tracts enhance seed germination using no choice feeding and laboratory germination experiments. Finally, we examine the extent to which goats consume the fruits of *E. acida* outside the protected area, and whether this consumption could account for the different stage structure of cacti between the protected and unprotected areas. To this end, we took advantage of a natural setting provided by the National Reserve, where large introduced herbivores do not have access to cactus populations, and an unprotected area next to the Reserve where goats forage freely. More specifically, in this study we address the two following questions: (1) What native species do eat the fruits and disperse the seeds of *E. acida* in the Reserve? (2) Do guanacos and goats eat the fruits and increase seed germination of *E. acida* after gut passage? Based on our results we discuss on the functional role of guanacos and goats for the seed dispersal process of *E. acida*, framing our results under Janzen and Martin's anachronism hypothesis as applied to the Chilean Mediterranean ecosystem.

Methods

Study site

This study was carried out within and in the area surrounding Las Chinchillas National Reserve, a semiarid protected area of north-central Chile (31°30'S, 71°06'W). The climate is a semiarid Mediterranean type, with most rainfall concentrated between June and August [20]. Mean annual precipitation is 185.0 mm, with ample variation across years, alternating between long droughts and unusual years of high rainfall, seemingly associated with El Niño Southern Oscillation events. The vegetation consists of thorny shrubs such as *Flourensia thurifera*, *Bahia ambrosioides* and *Porlieria chilensis* [21], the columnar cactus species *Trichocereus chiloensis* and *Eulychnia acida* and the spherical cacti *Cumulopuntia sphaerica* and *Eriosyce aurata* [12, 14, 22].

Frugivore recordings inside the Reserve

To identify the species involved in *E. acida* fruit consumption, fifty 1 × 1 m footprint-traps were established on hills of this Reserve when fresh fruits started to appear on the ground. One fresh fruit was placed as bait in the middle of each footprint-trap (mean fruit size ± SE: 49.4 ± 4.8 mm width, 48.5 ± 3.9 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.

No-choice feeding test

Only one species was found eating fruits of *E. acida* inside the Reserve, the brush-tailed rodent *Octodon degus*. To test for fruit consumption under captivity conditions, individuals of *O. degus* (Fig. 3) were captured with folding wire mesh live animal-traps (24 × 8 × 9 cm) baited with rolled oats and provided with cotton bedding. A total of 150 traps per night were set during five consecutive days, between 19:00 and 09:00 h, and checked every morning. The captured *O. degus* ($n = 33$) were maintained inside acrylic cages in an animal room with controlled temperature (25 °C) and relative humidity (45–65%). Animals were fed only with ripe fruits of *E. acida*, and after 3 days their feces were collected and visually inspected for cactus seeds. The capture of *O. degus* was performed under the permission of the Servicio Agrícola y Ganadero (resolution N° 1792 of April 2, 2012) and captive conditions were approved by the Ethics Committee of the Faculty of Medicine of University of Chile (CBA ≠ 0443 FMUCH).

No-choice feeding experiments were also carried out with local goat individuals ($n = 3$) and guanaco specimens from the Chilean National Zoo ($n = 11$) (Fig. 3). Goats were fed with *E. acida* fruits ad-libitum and no other food source was provided. For guanacos, *E. acida* fruits were given ad-libitum along with alfalfa hay and

Fig. 3 Putative consumers of *Eulychnia acida* fruits. *Lama guanicoe* (**a**), *Octodon degus* (**b**), and *Capra a. hircus* (**c**). *O. degus* photograph by Jorge Abarca

Mazuri® Llama chews. Goats and guanacos were fed with *E. acida* fruits for 2 days and their feces collected for two consecutive days after feeding. Feces were placed in paper bags and transported to the laboratory where seeds were manually extracted. Only seeds that were intact and whole were used in germination experiments.

Seed germination experiments

Controlled experiments were performed to determine the effect of gut passage on germination of *E. acida* seeds. Seeds were sown in plastic pots with gravel as a substrate, moistened with filtered water and placed in a growth chamber (PITEC, Model BIOREF-38) at *c.* 26 °C with a 14:10 h (day/night) photoperiod. Germination was recorded daily for 30 days, or until no germinating seeds were observed for more than 7 days. The criterion used to consider a seed germinated was radicle emergence. To assess germination, one seed was sown per pot ($n = 100$ pots per treatment). Seeds for the control treatment were obtained from ripe fruits. To test for differences in germination among treatments, the Kaplan-Meier survival function was estimated and then compared using a log-rank test with Bonferroni adjustment [23]. Analyses were performed in R software [24].

Recruitment of *E. acida* in the field

To assess juvenile recruitment, we recorded the number of young (less than 30 cm height), and adult individuals of *E. acida* in three patches of similar size inside the Reserve (Patch 1: 0.80 ha, Patch 2: 0.68 ha, Patch 3: 0.65 ha) and outside the Reserve (Patch 1: 0.61 ha, Patch 2: 0.75 ha, Patch 3: 0.75 ha). The areas were approximately 1 km apart and have similar characteristics of exposure, slope, vegetation composition and structure. Young individuals of *E. acida* were intensively searched on bare soil and under the bushes. A χ^2 test was performed to evaluate differences in the stage structure between areas.

Findings

Frugivore species inside the Reserve

Three types of footprints were identified on the footprint-traps, corresponding to two bird species, the Chilean tinamou *Nothoprocta perdicaria* ($n = 19$ footprint-traps) and the Chilean mockingbird *Mimus thenca* ($n = 15$ footprint-traps), and one rodent species, the rodent *O. degus* ($n = 11$ footprint-traps). Only *N. perdicaria* can be suggested as a potential bird fruit consumer as fruits were found with signs of having been pecked ($n = 6$), albeit not enough to swallow seeds. On the other hand, *M. thenca* only pecked the fruit once; therefore, the evidence of fruit intake is insufficient. Only *O. degus* ate the fruits completely, carried the fruits to their caves, leaving only fruit remnants at the end of the thread ($n = 8$ footprint-traps).

Effect of gut passage on seed germination

In the no-choice feeding experiments, all the tested *O. degus* individuals consumed the whole fruit. Only 15 seeds were recovered, corresponding to 0.011% of the total ingested seeds (considering a mean of 1930 seeds/fruit). Because this rodent species destroyed most of the seeds passing through their digestive tracts, it cannot be considered a legitimate disperser for *E. acida* (sensu [25]). Both goats and guanacos ate fruits of *E. acida*, and many whole seeds were found in their feces. Seeds defecated by goats had the highest germination of all treatments (60%) but did not differ from the control (52%) ($\chi^2 = 1.0$, $P = 0.98$) (Fig. 4). Seeds from guanacos germinated to a much lower extent than those from goats (13%) ($\chi^2 = 50.2$, $P < 0.001$). Likewise, seeds defecated by *L. guanicoe* germinated significantly less than control seeds ($\chi^2 = 36.4$, $P < 0.001$).

Eulychnia acida recruitment

Regarding cactus recruitment, there was a lower proportion of young individuals inside than outside the Reserve

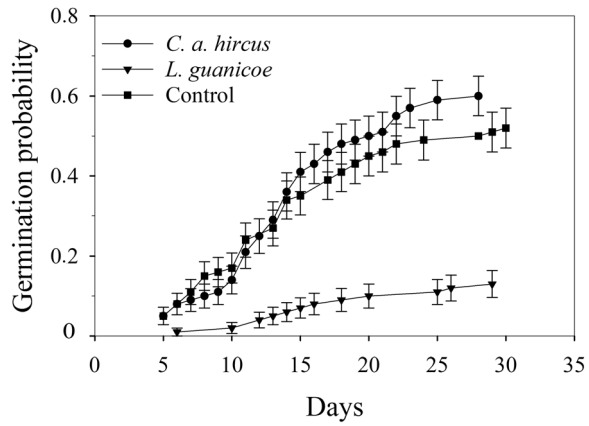

Fig. 4 Kaplan-Meier estimates of survivorship for germination of *Eulychnia acida* seeds after guanaco, goat, and control treatments

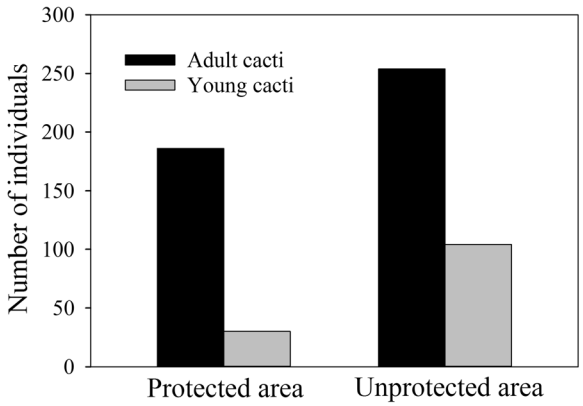

Fig. 5 Number of young and adult individuals of *Eulychnia acida* in two contrasting locations considering caprine livestock presence: protected and unprotected areas (inside and outside Las Chinchilllas National Reserve, respectively)

($\chi^2 = 17.31$, $P < 0.001$, Fig. 5). A total of 30 young and 186 adult individuals were recorded in 2.15 ha inside the Reserve, while outside the protected area a total of 104 young and 254 adult individuals were recorded in 2.11 ha. This result suggests that *E. acida* finds better conditions for dispersal and/or germination outside than inside the Reserve, which is likely related to the presence of goats outside.

Discussion

In this study, we examined the consumers of *E. acida* fruits in a protected area to determine the native species potentially involved in seed dispersal of this cactus species. We detected fruits with marks of having been pecked by two bird species, *N. perdicaria* and *M. thenca*. However, these birds did not eat enough of the fruit to ingest seeds, therefore they cannot be considered legitimate seed dispersers (sensu [25]). A previous study indicated that birds behave as seed dispersers of *Trichocereus chiloensis* (sin. *Echinopsis chiloensis*) a columnar cactus with ripe fruits that stay open on the cactus branch, exposing the sugared pulp to seed dispersers [26]. Unlike *T. chiloensis*, the fruits of *E. acida* are indehiscent and present an acidic pulp [27], which is not preferred by birds. Our evidence indicates that *O. degus* was the only mammal species consuming fruits of *E. acida* during the sampling time. However, almost all seeds ingested by *O. degus* were destroyed and only a few seeds could be recovered from their feces. This result was in line with a previous generalization that rodents behave as seed predators, as they kill most of the seeds through the gut passage [1]. In the light of these findings, we could conclude that the two-bird and one rodent species here examined cannot be considered legitimate seed dispersers (sensu [25]).

Regarding the seed dispersal syndrome concept, fruits often show characteristics associated with the type of seed disperser involved [8]. Our results suggest that fruits of *E. acida* are not suitable for most native fruit consumers present in the Reserve. Because our data indicate that *N. perdicaria*, *M. thenca* and *O. degus* are not legitimate seed dispersers, it is unlikely that fruit traits of *E. acida* do fit to the feeding preference of the native Chilean fauna at present. By contrast, goats eat fruits of *E. acida*, and seed gut passage does not affect germination negatively. As goats often defecate at random in the field [28], seeds may fall in potentially safe places by chance only. Therefore, we suggest that goats could potentially enhance population recruitment of *E. acida,* which may account, at least in part, for the higher density of young *E. acida* individuals observed outside than inside the Reserve.

Species of the cactus family often have very low recruitment rates by both vegetative and sexual reproduction in natural conditions [29, 30]. In consequence, seed dispersers may play an important role as biotic agents that enhance the chance of germination and population recruitment [4]. Other studies have described goats as a potential seed disperser for cactus species in Mexico [16, 17], where goat husbandry is one of the main economic activities. This is also the case in north-central region of Chile (27°22’ S, 70°19’ W to 33°3’ S, 71°38’ W), where goat overstocking is one of the main activities contributing to desertification [31, 32]. Contrary to the general assumption that goat activity conveys mostly habitat loss and degradation, the present study suggests they may act as important dispersal agents of *Eulychnia* populations.

Several large herbivore mammals such as Gomphotheres became extinct in Pleistocene times [33], and probably some of them ate cactus fruits as they have been suggested to have generalist trophic habits [34].

One of the few large-sized mammal groups that survived megafauna Pleistocene extinctions was the genus *Lama* [35]. It is likely that *Lama* species were involved in the seed dispersal process of *Eulychnia* species until the arrival of the Spaniards, during the XVI century. Then, guanaco populations rapidly declined in number and its distribution is mostly circumscribed to high elevation areas in the Andes Range due to overhunting and occupation of pastures by cattle that consumed the native vegetation [36, 37]. Because the geographical distribution of *L. guanicoe* does not overlap with the Reserve location at present [38], we hypothesize that in the last centuries goats may have played a surrogate functional role for the seed dispersal process of *E. acida*. The experimental evidence that unlike *L. guanicoe*, goats do not decrease the seed germination of *E. acida* after gut passage, suggests that in the absence of native frugivore species introduced goats might play an important role in the seed dispersal process of the endemic cactus *E. acida*, extending Janzen and Martin's (1982) anachronism hypothesis to the Chilean Mediterranean ecosystem.

Conclusions

Our results indicate that fruits of *E. acida* are pecked by *N. perdicaria* and *M. thenca*, and eaten by the rodent *O. degus*. However, none of these species could be considered a legitimate seed disperser. Unlike *L. guanicoe*, the goat *C. a. hircus*, a species introduced by humans in semiarid Chilean ecosystems, consumed fruits of *E. acida* without decreasing seed germination. Indeed, our data indicate that variation in stage structure, a proxy of plant recruitment, between protected and unprotected areas may result from goat activity favoring cactus recruitment in areas where native dispersers are no longer present. Overall, the results of this study are compatible with Janzen and Martin's (1982) anachronism hypothesis for tropical ecosystems, extended to the Chilean Mediterranean ecosystem.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Authors' contributions

Experimental design: CBM, RM, RAC, CSC. Fieldwork: RAC and CSC. Performed the experiments: CSC and RAC. Data analysis: RAC, CSC, CBM, RM and AVB. Manuscript preparation: RAC, CSC, CBM, RM and AVB. All authors read and approved the final version of the manuscript.

Ethics approval and consent to participate

The captive conditions of *O. degus* were approved by the Ethics Committee of the Faculty of Medicine of University of Chile (CBA ≠ 0443 FMUCH).

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Publisher's Note

Author details

[1]Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Ñuñoa, Santiago, Chile. [2]Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, 04510 Coyoacán, Distrito Federal, Mexico.

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