

# Ecological efficiency and legitimacy in seed dispersal of an endemic shrub (*Lithrea caustica*) by the European rabbit (*Oryctolagus cuniculus*) in central Chile

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## Abstract

The European rabbit (*Oryctolagus cuniculus*) is an alien herbivore in central Chile. Although its diet is poorly studied, this rabbit is known to consume native fruits and seeds, and thus it could act as a seed-dispersal agent. We evaluated the effect of endozoochory by rabbits on the survival and germination of seeds of a native shrub (*Lithrea caustica*, Anacardiaceae), as well as its consequences for seed dispersal. We extracted seeds by hand from parental shrubs, and compared the germination dynamics of seeds passing once and twice throughout the rabbit's gut (simulating its coprophagy) versus control treatments (seeds not consumed). Additionally, in permanent 2 × 2 m sampling plots placed in the wild, we evaluated the abundance of *L. caustica* seedlings and of its seeds in rabbit droppings. Results indicate that rabbits reduced seed survival to 82% on average with the first gut passage, and to an additional 52% with a second passage. Nevertheless, germination variables such as initiation time and germination, as well as final germination rate, increased significantly in comparison to non-ingested seeds. Sampling plots showed that *L. caustica* seedlings were concentrated principally underneath woody patches, which are then regarded as safe sites. Outside shrub cover, seedling abundance small, this indicates that open places are unsafe sites. We recorded that feces (and seeds contained) were deposited in higher proportion beneath woody cover. Thus, the native shrub *L. caustica* may be dispersed by alien rabbits through endozoochory, which provides legitimacy and efficiency in this dispersal service. Alien rabbits may fill a similar role played by native mammals, which have been reduced in abundance by human agency in central Chile. We suggest that the generalist syndrome, common among plants and dispersers, may be an arena of positive effects in ecological interactions between alien and native species.

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**Keywords:** Alien species; Endozoochory; Germination; Herbivorous mammals; *Lithrea caustica*; Mediterranean ecosystem

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## 1. Introduction

Alien species are said to affect the structure and function of native ecosystems, usually in undesirable ways (Elton, 1958; Levine et al., 2003; Parker et al., 1999; Wilcove et al., 1998; Williamson, 1996). This negative

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view of biological invaders owes to a focus on antagonistic interactions such as competition, predation and parasitism, and to a neglect of potentially mutualistic plant–animal interactions with native species (Christian, 2001; Grosholz, 2005; Richardson et al., 2000; Simberloff and Von Holle, 1999), such as seed dispersal and pollination. Particularly in seed-dispersal interactions, it is recognized that both fleshy fruits and frugivorous vertebrates show ample generalism (Howe and Smallwood, 1982), thus leading native plants to interact with numerous frugivorous animals, including alien species.

Many alien herbivorous mammals consume native fruits and seeds in their native range (Crawley, 1997; Herrera, 1995; Homolka, 1988; Howe and Smallwood, 1982; Janzen, 1984), being considered endozoochorous seed dispersers because they defecate germinable seeds at variable distances from parental plants (Corlett, 1998; Cosyns et al., 2005; Malo and Suarez, 1995; Malo et al., 2000; Maron and Vilà, 2001; Myers et al., 2004; Olf and Ritchie, 1998; Pakeman et al., 1999, 2002; Poulsen et al., 2002). Several studies have focused on livestock (cattle, sheep, goats, horses, donkeys, pigs) dispersal of herb seeds (Cosyns et al., 2005; Pakeman et al., 2002; Vellend et al., 2003; Welch, 1985), and show that dispersal occurs because germinable seeds are dropped in feces, despite their digestive treatment having reduced somehow the germinative response (Cosyns et al., 2005; Pakeman et al., 1999, 2002). However, little attention has been directed to the quality component of the seed-dispersal service in plant–herbivore systems (Olf and Ritchie, 1998; Wang and Smith, 2002).

Seeds ingested by herbivorous mammals must move through plant demographic barriers that finally determine their establishment (Wang and Smith, 2002). Thus, quantifying where consumed seeds are dropped and how endozoochory affects seed survival and germination constitute two integrated components of the quality of dispersal service and its demographic consequences for plants (Bustamante and Canals, 1995; McKey, 1975). Dispersal legitimacy quantifies the proportion of ingested seeds that are defecated in viable and/or germinable conditions (Herrera, 1989), while dispersal efficiency quantifies the proportion of seeds defecated in safe sites (Reid, 1989). In one extreme, an alien herbivorous mammal could defecate unviable seeds (illegitimate disperser, or seed predator) or in unsafe sites (inefficient disperser), thus increasing seed mortality. On the other extreme, seeds could be defecated viable (legitimately) and in suitable sites for their germination and establishment (efficiently). Characterizing these attributes of seed-dispersal services by alien mammals enables to understand their demographic consequences for the plants consumed.

The European rabbit (*Oryctolagus cuniculus*) is an introduced herbivore in several regions around the world, including the Americas, Great Britain, Africa, Australia, New Zealand, and countless small islands (Armstrong, 1982; Flux, 1994; Flux and Fullagar, 1992). In the majority of these regions, European rabbits are considered a pest due to their deleterious effects on native vegetation (Bullock et al., 2001; Cooper and Brooke, 1982; Courchamp et al., 2003; Jaksic, 1998; Merton et al., 2001; Selkirk et al., 1983; Taylor, 1968; Thompson and King, 1994). Most studies focusing on germination of seeds defecated by rabbits have been conducted in their original range in Europe (Cosyns et al., 2005; Dellafiore et al., 2006; Malo and Suarez, 1995; Malo et al., 2000; Pakeman et al., 2002). Observations in central Chile by Hoffman et al. (1989) indicate that European rabbits consume seeds and fleshy fruits of native woody plants, but until now it has not been evaluated whether rabbits contribute to their dispersal.

During fieldwork in central Chile, we detected intact and germinating seeds of the native shrub *Lithrea caustica* (Anacardiaceae) inside European rabbit feces. We used a combination of observational and experimental procedures to evaluate the quality of seed-dispersal services rendered by rabbits to *L. caustica*. Specifically, we quantified: (a) dispersal efficiency, determining whether rabbits defecate seeds in safe sites for establishment, and (b) dispersal legitimacy, quantifying the rate at which seeds of *L. caustica* are dropped in germinable condition. Additionally, we examined the consequences of single and double transit of seeds through the gut, because *O. cuniculus* is coprophagous (it eats its own feces).

## 2. Methods

### 2.1. Study area

We conducted our study in Estación de Investigaciones Ecológicas Mediterráneas (EDIEM; 33°23'S, 70°31'W) located 20 km east of Santiago on the Andean foothills. This study site occupies 835 ha, with elevations ranging from 1050 to 1915 m. The climate is Mediterranean (di Castri and Hajek, 1976), with mean

annual rainfall of 376.4 mm, concentrated during the austral winter months (June–August). The mean temperature is highest from December to March (corresponding to the austral summer) and lowest from June to August (the austral winter). Details of the climate and habitat conditions at the study site are available at [www.bio.puc.cl/sca/](http://www.bio.puc.cl/sca/).

The site is covered by sclerophyllous vegetation, which physiognomically may be described as an evergreen shrubland (named matorral in Chile), one of the most characteristic vegetation formations in central Chile (Gajardo, 1994; Rundel, 1981). The composition and physiognomy of the matorral are determined by human influence (Rundel, 1981), which produces fragments or patches of woody flora with variable composition and extension (Fuentes et al., 1984). These patches are surrounded by a herbaceous layer with mixed native and alien herbs, which is distributed mainly between matorral fragments, in the open areas away from shrubs (Fuentes et al., 1984, 1986). *L. caustica* is a dominant shrub in these fragments, with cover ranging 12–42% depending on slope and orientation. Other shrubs such as *Kageneckia oblonga* (Rosaceae), *Colliguaja odorifera* (Euphorbiaceae), *Baccharis rosmarinifolia* (Asteraceae), *Quillaja saponaria* (Rosaceae), *Podanthus mitique* (Asteraceae), *Acacia caven* (Fabaceae), and *Azara dentata* (Flacourtiaceae) are present in the fragments as well.

## 2.2. Plant and herbivore species

*L. caustica* (known as litre) is an endemic sclerophyllous evergreen shrub in Chile and is distributed between 32 and 39°S (Rodríguez et al., 1983). This species is common in varied vegetation formations, such as semi-arid coastal scrub, evergreen scrubland, and evergreen forest (Gajardo, 1994), being particularly abundant in the matorral formation. The flowering and fruiting periods occur during September–December and February–March, respectively (Rodríguez et al., 1983), although fruits may be present in parental plants during all year. The fruit is a hard drupe containing only one seed with a lentil form (5–6 mm long, 3–4 mm wide). The fruit is consumed and potentially dispersed by native birds and foxes (Hoffmann et al., 1989; Jaksic et al., 1980; León-Lobos and Kalin-Arroyo, 1994; Rodríguez et al., 1983), but these consumers have become scarce in the matorral exposed to recurrent human influence, especially so in the study site (Jaksic, 2001).

The European rabbit *O. cuniculus* was introduced to central Chile and is now distributed between 27 and 41°S, ca. 2000 km along the country (Jaksic et al., 2002). In the matorral, studies on rabbit ecology have focused on its importance as a browser and grazer (Fuentes et al., 1983, 1984; Holmgren, 2002; Jaksic and Fuentes, 1980) and as prey of native predators (Jaksic and Fuentes, 1991; Jaksic and Ostfeld, 1983; Jaksic and Soriquer, 1981). As a herbivore, the rabbit limits the recruitment of native woody plants and herbs to underneath nursery shrubs (Fuentes et al., 1984, 1986; Jaksic and Fuentes, 1980), because its foraging activity occurs mainly in open areas between shrubby patches (Fuentes et al., 1983; Jaksic et al., 1979). As noted by Hoffman et al. (1989), rabbits also feed on fruits and seeds.

## 2.3. Spatial distribution of dispersed seeds

During the austral summer of 2006, we quantified the efficiency of rabbits as seed dispersers of *L. caustica* by examining the spatial pattern of fecal seed deposition. Because of its harsh conditions of high temperature and low humidity, the austral summer constitutes a critical and limiting period for the establishment of seedlings. We recognized two habitat patch types: the exposed area corresponding to a herbaceous matrix located between woody patches (distant 15–20 m from woody fragments), and the sheltered area corresponding to sites underneath woody patches (1–3 m inside of fragments). These patches were defined according to their microclimatic and ecological relevance for the establishment of native plants—including *L. caustica*—according to previous studies at the study site (del Pozo et al., 1989; Fuentes et al., 1984, 1986; Jimenez and Armesto, 1992).

In each patch, we set 50 permanent plots (2 × 2 m, totaling 100 plots). Initially, plots were marked for future visits and then all old rabbit feces were removed. Monthly, we collected fresh rabbit feces from every plot and recorded the number of seeds of *L. caustica* in each fecal pellet. Defecated seeds were placed in petri dishes (five per dish), with moist blotting paper during 3 days, and later subjected to the tetrazolium test (Barton, 1961), thus determining their viability. We estimated the efficiency of rabbits as seed dispersers of *L. caustica* by calculating the proportion of seeds dropped in viable condition to the two habitat patches recognized.

Additionally, we sampled the abundance of recently emerged seedlings of *L. caustica* in both habitat patches. We used 100 other quadrates ( $2 \times 2$  m) equally distributed in exposed and sheltered areas, and recorded the number of seedlings of *L. caustica*. Seedlings were recognized by their size ( $< 20$  cm tall) and special attention was paid to excluding ramets.

#### 2.4. Endozoochory effects on germination and survival

A sample of five males and three females of wild-caught European rabbits (mean body mass  $\pm$  S.D. for males:  $760 \pm 240$  g, for females:  $766 \pm 380$  g) were captured at EDIEM. Rabbits were weighted and maintained in captivity in cages of  $0.8 \times 0.4 \times 0.4$  m. They were acclimated during 7 days with commercial rabbit food pellet (0.1 kg of pellets/day/rabbit twice a day) and water *ad libitum*. Daily, all rabbits were weighted to control for drastic changes in body mass.

##### 2.4.1. Feeding experiments

We collected  $> 2000$  mature fruits of *L. caustica* from 50 different plants. Their pericarp was manually removed, storing the seeds in paper bags and then maintained at  $10^\circ\text{C}$ . Twelve randomized sub-samples of seeds (50 seeds for each sub-sample, totaling 600 seeds) were set apart for experimental tests. Together with food pellets, we offered 50 seeds of *L. caustica* to each rabbit. Rabbits consumed all seeds in variable periods ranging 1–3 days. During this period, all rabbit feces were collected and the seeds removed manually. Then, four rabbits were randomly chosen to re-consume their defecated seeds, simulating the double passage through the digestive tract that occurs during coprophagy. For this purpose, seeds were offered together with commercial pellet, as in the previous experiment. Thus, we obtained three pre-germinative treatments: intact and defecated seeds, the latter with single or double passage throughout the rabbit digestive tract, which were subsequently used in the germination experiments described in the following text.

##### 2.4.2. Germination experiments

Intact and defecated seeds were subjected to germination trials in petri dishes (five per dish), in a greenhouse (Pontificia Universidad Católica de Chile; temperature:  $35\text{--}15^\circ\text{C}$ ; photoperiod: 16/8). Each dish had blotting paper periodically moistened. Daily, we recorded seed germination defined by radicle emergence. This experiment lasted 2 months, and at its end the non-germinated seeds were submitted to the tetrazolium viability test (Barton, 1961). In each pre-germinative treatment, we determined four indices of germination dynamics: (a) initiation time of germination (ITG), which is the average time in days to recording the first germination among dishes; (b) accumulative germination (AG), which is the cumulative frequency of germination determined daily; (c) mean time of germination (MTG), which is the average time in days to recording 50% of the seeds germinated among dishes; (d) final germination rate (FGR), which is the percentage of germination at the end of the experiment.

#### 2.5. Data and statistical analyses

We compared the frequency and density of rabbit feces, defecated seeds, and seedlings established, according to exposed and sheltered patches as the grouping factor. Frequencies were analyzed by means of *G*-test, whereas densities were analyzed using Mann–Whitney *U*-test (Sokal and Rohlf, 1994). In order to compare seed survival after gut passage, we carried out a *G*-test upon a contingency table (Sokal and Rohlf, 1994). Here, we used the final survival frequency (viable + germinated seeds) grouped into three seed categories: intact, endozoochory (one passage throughout gut), and coprophagical (two passages).

The effect of gut passage on germination dynamics (ITG and MTG) was assessed by a Kruskal–Wallis *H*-test (Sokal and Rohlf, 1994), with variables grouped according to the number of gut passages (0, 1 and 2) as factors. We used a *G*-test to compare FGR and repeated-measures ANOVA (MGLM; Sokal and Rohlf, 1994) in the accumulated germination. The relative germination accumulated (arcsine square-root transformed) was used as dependent variable, using four replicates (four rabbits) by treatment: intact, endozoochory, and coprophagical seeds. Subsequently, we used the *a posteriori* multiple comparisons test (*T*-test) for recognizing

differences among these treatments (Sokal and Rohlf, 1994). All these analyses were made using version 6.0.1 of Systat.

### 3. Results

#### 3.1. Spatial distribution of defecated seeds and seedlings

A total of 28 seedlings of *L. caustica* were recorded among the 100 quadrates. Twenty-five of them (89.2%) were found in sheltered patches and only three (10.8%) in exposed patches, with a mean  $\pm$  S.D. of  $0.5 \pm 0.7$  and  $0.06 \pm 0.2$  individuals/2 m<sup>2</sup>, respectively (Table 1). We detected statistical differences in seedling frequency between both patches ( $G = 19.7$ ,  $P < 0.05$ , d.f. = 1), nearly nine times higher in sheltered than in exposed patches.

The number of fresh rabbit feces collected was 2990, with 1580 (52.8%) from exposed patches and 1410 (47.2%) from sheltered patches, which is statistically different ( $G = 9.6$ ,  $P < 0.05$ , d.f. = 1). The frequency of seeds defecated in both patches was different as well ( $G = 11.5$ ,  $P < 0.05$ , d.f. = 1), with 66.6% of seeds deposited in sheltered and 33.4% in exposed patches (Table 1). All (100%) seeds retrieved from rabbit feces were viable.

#### 3.2. Endozoochory effects on germination and seed survival

Seeds with a single gut passage had a final survival of 82%, ranging 76–90% (Table 2). Thus, digestive processing destroyed 18% of them. For coprophagical seeds (two gut passages), final survival was 52%, ranging 40–62%. An increase in destroyed seeds is clear here (48% on average). The percentage of final survival of seeds in both treatments shows statistical differences according to the number of passages throughout rabbit's digestive tract ( $U = 0$ ,  $P = 0.02$ ), indicating that seed survival depended on the number of gut passages. All defecated seeds that were physically intact at defecation got to germinate or came up positive in the tetrazolium test (Table 2).

Accumulated germination according to different treatments is shown in Fig. 1. The curves show a marked increase in germination of defecated seeds while intact seeds display a slower germination rate. Seeds consumed by rabbits show earlier germination, 5–6 days on average, in contrast to 35 days among intact seeds (Table 2). Statistical differences were found between consumed and intact seeds according to ITG ( $T = 6.8$ ,  $P = 0.001$ ). FGR in intact seeds was 5% on average (range 2–10%; Table 2), while consumed seeds (single and double passage) had a significantly higher FGR (75% and 67%, respectively,  $U = 0$ ,  $P = 0.006$ ; Table 2). Finally, we did not find differences in MTG between treatments, ranging 33–36 days long ( $T = 8.7$ ,  $P = 0.63$ ; Table 2).

Intact seeds showed a slower germination rate, reaching an average of 5.5% (range 2–10%) at the end of trials (Table 2), while endozoochorous seeds (single and double passage) displayed a higher rate of germination and of final germination (74.9% and 63.2%, respectively; Table 2). Repeated-measures ANOVA showed significant differences between the dynamics of germination according to pre-germinative treatment

Table 1

Spatial distribution of *L. caustica* seedlings and of rabbit-defecated seeds in two habitat patches (sheltered and exposed) in Chilean matorral

Habitat patches	Seedlings		Defecated seeds	
	<i>n</i> (%)	Abundance	<i>n</i> (%)	Abundance
Sheltered	25 (89.2)	$0.50 \pm 0.6$	68 (66.6)	$1.36 \pm 2.0$
Exposed	3 (10.8)	$0.06 \pm 0.2$	34 (33.4)	$0.68 \pm 0.8$
Test		$G = 19.7$ ( $P < 0.05$ )		$G = 11.5$ ( $P < 0.05$ )

Abundance is expressed as mean  $\pm$  S.D.

Table 2

Indices of germination for seeds of *L. caustica* in response to none, single, and double passage throughout rabbit digestive tract

Indices	None	Single	Double
Seed survival (%)	100	82 (76–90)	52 (40–62)
Initiation time to germination (ITG; days)	37 (30–46)	7 (4–10)	8 (2–15)
Mean time to germination (MTG; days)	52 (45–56)	48 (49–50)	46 (37–52)
Final germination rate (FGR; %)	5 (2–10)	75 (58–91)	65 (58–75)

Range values are indicated in parentheses.

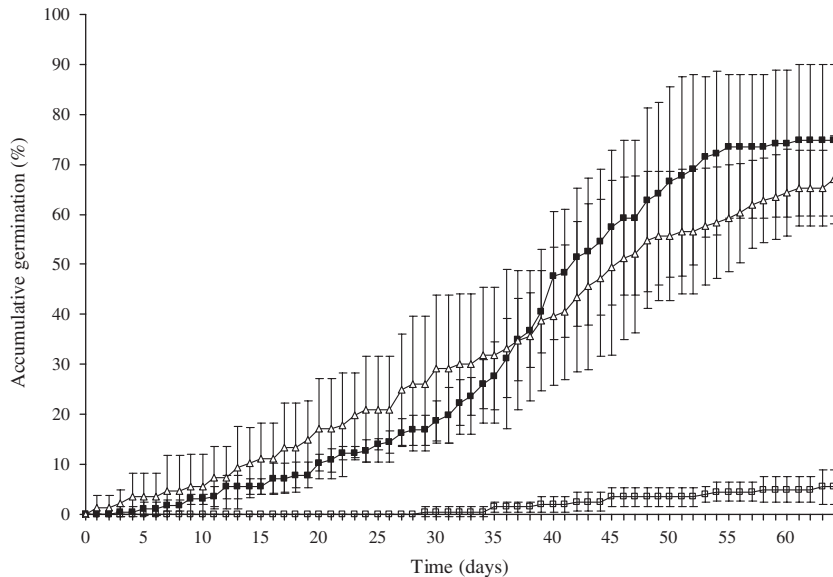


Fig. 1. Accumulative germination (mean  $\pm$  S.E.) of *L. caustica* seeds. Black squares: seeds passed once throughout rabbit digestive tract; white triangles: seeds passed twice; white squares: seeds not ingested by rabbits.

(Table 3). Interestingly, the *a posteriori* test detected differences due to intact-seed treatment ( $P < 0.001$  in both comparisons), without differences between endozoochory- and coprophagy-treatment ( $T = 1.3$ ,  $P = 0.989$ ).

#### 4. Discussion

Overall, our results indicate that *L. caustica* is dispersed by rabbit endozoochory, the legitimacy and efficiency of this dispersal service being maximized when the seeds experience a single gut passage and are dropped inside woody fragments in the matorral. Passage of *L. caustica* seeds through the gut of *O. cuniculus* reduces seed survival but increases germination rate and final germination as well. Considering that rabbits perform coprophagy (eat their own feces), differences in these parameters could be expected according to the number of gut passages. Indeed, a double passage (simulating coprophagy) decreased significantly seed survival by 30%, and decreased germination rate and final germination by 10% on average. Complementarily, rabbits defecated viable seeds into the two habitats patches defined here, exposed and sheltered. Still, seeds defecated by rabbits were more frequent in sheltered than in exposed patches (66% versus 34%, respectively).

According to previous research, sheltered patches in the Chilean matorral are safe sites for the establishment of woody plants, because they enable escape from herbivory by mammals (Armesto and Pickett, 1985; Fuentes et al., 1984; Jaksic and Fuentes, 1980; Jimenez and Armesto, 1992) and from desiccation during the austral summer (del Pozo et al., 1989). Thus, the 28 seedlings of *L. caustica* found in our 100 quadrates confirm that areas underneath woody patches are safer, at least during early steps of establishment: 89% of the seedlings were in sheltered patches, while only 11% were in exposed patches. It is important to remark that the

Table 3

Univariate repeated-measures ANOVA showing the effects of pre-germinative treatments, time, and interaction between time and pre-germinative treatments

Source	d.f.	F	P
Between subjects			
Pre-germinative treatments	2	25.1	<0.001
Error	9		
Within subjects			
Time	5	140.3	<0.001
Time × pre-germinative treatments	10	29.7	<0.001
Error	45	28.2	

regeneration of woody plants of the Chilean matorral is strongly limited by herbivory and drought, resulting in a scarce number of seedlings that can recruit annually (Fuentes et al., 1984, 1986; Jimenez and Armesto, 1992); thus, the 28 seedlings found in our quadrates represent a considerable proportion of the seedlings recruited that year. Although about half the rabbits feces were found in either habitat patch, two-thirds of the defecated seeds were found in the sheltered patch. Perhaps rabbit droppings decompose more quickly in the exposed patch.

The rabbit-caused mortality of *L. caustica* seeds was due to chewing, judging from seed fragments found in feces. In contrast, all physically intact seeds retrieved from rabbit feces were viable. On the other hand, germination is likely associated to mechanical and chemical scarification (Cabello, 1979), when the hard coats of the seed are partially removed during the digestive process, as has been documented in other members of Anacardiaceae (Cabello, 1979, 1990; Castro et al., 1994; Verdú and García-Fayos, 2002). Other authors have suggested that alien herbivores (including European rabbits) facilitate the spread of alien herbs in Mediterranean-type communities all over the world (Arroyo et al., 2000; Kruger et al., 1989), implicitly invoking the invasional meltdown hypothesis (Simberloff and Von Holle, 1999) of positive effects among non-native species. However, our results show that native plants are susceptible to seed dispersal by alien species as well. Further, we have also recorded seeds of native shrubs *Cryptocarya alba* (Lauraceae), *Azara lanceolata* (Flacourtiaceae), and *Peumus boldus* (Monimiceae), as well as of native herbs and monocots, in feces of European rabbits.

The endemic *L. caustica* is a dominant shrub in the Chilean matorral (Gajardo, 1994). Although several species of native vertebrates (including birds, rodents, and foxes) have been described as frugivorous and as potential seed dispersers of *L. caustica* in central Chile (Hoffman et al., 1989), little quantitative evidence is available. León-Lobos and Kalin-Arroyo (1994) documented that *L. caustica* seeds obtained from fox feces (*Pseudalopex* sp.) exhibit delayed germination in comparison with seeds obtained directly from trees, and that foxes did not affect the final percentage of germination. Interestingly, not only foxes but several other vertebrates that potentially disperse seeds of *L. caustica* have been reduced in abundance in our study site by increasing human interference over the last 25 years (Jaksic, 2001). This is not the case of rabbits, which now thrive in the study site and in the matorral in general, and thus may have an unsuspected role as dispersers of *L. caustica* and other plants, and may be functionally replacing native seed dispersers.

The European rabbit is considered a biological pest in its exotic ranges (Flux, 1994; Thompson and King, 1994), including central Chile (Jaksic and Fuentes, 1991). But according to our results, its ecological role may be more complex than previously thought. First, *O. cuniculus* affects plants by browsing or grazing them, choosing some and ignoring other species, thus exerting a significant role in determining the coexistence and structure of the plant communities where it lives (Castro and Jaksic, unpublished data; Chapuis et al., 2004; Zavaleta et al., 2001). Second, seed dispersal by rabbits may be a more generalized phenomenon, especially for plants with small seeds, which are the most likely candidates to survive digestion (Cosyns et al., 2005; Malo et al., 2000; Myers et al., 2004). Seed dispersal by rabbit exozoochory may be important as well, but virtually nothing is known about this phenomenon in its exotic ranges (Malo and Suarez, 1997). Thus, the ecological role of the European rabbit—and of other alien species now considered biological pests—should be revisited

in the light of more complete ecological evidence. Critical research involves a quantification of the seed-dispersal services (if they exist) that alien species may perform for both native and exotic plants.

We conclude that European rabbits act as legitimate and efficient seed dispersers of the Chilean native shrub *L. caustica*, performing a similar role to native vertebrates that have been reduced in abundance by human agency in central Chile. Following Richardson et al. (2000), we suggest that the generalist syndrome, common among plants and dispersers, may be an arena of positive ecological effects between native and alien species.

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## References

- Armesto, J.A., Pickett, S.T.A., 1985. A mechanistic approach to the study of succession in the Chilean matorral. *Revista Chilena de Historia Natural* 58, 9–17.
- Armstrong, P., 1982. Rabbit (*Oryctolagus cuniculus*) on islands: a case study of successful colonization. *Journal of Biogeography* 9, 353–362.
- Arroyo, M.T.K., Marticorena, C.M., Matthei, O., Cavieres, L., 2000. Plant invasions in Chile: present patterns and future predictions. In: Mooney, H.A., Hobbs, R. (Eds.), *Impact of Global Change on Invasive Species*. Island Press, Washington, DC, pp. 385–421.
- Barton, L.V., 1961. Seed Preservation and Longevity. Leonard Hill Limited, London, UK.
- Bullock, D.J., North, S.G., Dulloo, M.E., Thorsen, M., 2001. The impact of rabbit and goat eradication on the ecology of Round Island, Mauritius. In: Veitch, C.R., Clout, M.N. (Eds.), *Turning the Tide: The Eradication of Invasive Species*. IUCN SSC Invasive Species Specialist Group, IUCN, Gland, Switzerland and Cambridge, UK, pp. 53–63.
- Bustamante, R.O., Canals, M., 1995. Dispersal quality in plants: how to measure efficiency and effectiveness. *Oikos* 73, 133–136.
- Cabello, A., 1979. Estudio anatómico y de germinación en litre (*Lithrea caustica* (Mol.) H. et Arn.). Tesis de Ingeniería Forestal, Facultad de Ciencias Forestales, Universidad de Chile, Santiago, Chile.
- Cabello, A., 1990. Propagación de especies pertenecientes a los bosques esclerófilos y espinosos de la zona central de Chile. *Apuntes Docentes*, vol. 3. Facultad de Ciencias Agrarias y Forestales, Departamento de Silvicultura, Universidad de Chile, Santiago, Chile, pp. 56–74.
- Castro, S.A., Silva, S.I., Meserve, P.L., Gutiérrez, J.R., Contreras, L.C., Jaksic, F.M., 1994. Frugivoría y dispersión de semillas de pimienta (*Schinus molle*) por el zorro culpeo (*Pseudalopex culpaeus*) en el Parque Nacional Fray Jorge (IV Región, Chile). *Revista Chilena de Historia Natural* 67, 169–176.
- Chapuis, J.L., Frenot, Y., Lebouvier, M., 2004. Recovery of native plant communities after eradication of rabbits from the subantarctic Kerguelen Islands, and influence of climate change. *Biological Conservation* 117, 167–179.
- Christian, C.E., 2001. Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature* 413, 635–639.
- Cooper, J., Brooke, R.K., 1982. Past and present distribution of the feral European rabbit *Oryctolagus cuniculus* on southern African offshore islands. *South African Journal of Wildlife Research* 12, 71–75.
- Corlett, R.T., 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews* 73, 413–448.
- Cosyns, E., Delporte, A., Lens, L., Hoffmann, M., 2005. Germination success of temperate grassland species after passage through ungulate and rabbit guts. *Journal of Ecology* 93, 353–361.
- Courchamp, F., Chapuis, J.L., Pascal, M., 2003. Mammal invaders on islands: impact, control and control impact. *Biological Reviews* 78, 347–383.
- Crawley, M., 1997. *Plant Ecology*. Blackwell Science, New York, USA.
- Dellafiore, C.M., Valles, S.M., Fernandez, J.B.G., 2006. Rabbits (*Oryctolagus cuniculus*) as dispersers of *Retama monosperma* seeds in a coastal dune system. *Ecoscience* 13, 5–10.
- Del Pozo, A.H., Fuentes, E.R., Hajek, E.R., Molina, J.D., 1989. Zonación microclimática: efecto de los manchones de arbustos en el matorral de Chile central. *Revista Chilena de Historia Natural* 62, 85–94.
- Di Castri, F., Hajek, E.R., 1976. *Bioclimatología de Chile*. Universidad Católica de Chile, Santiago, Chile.
- Elton, C.S., 1958. *The Ecology of Invasions by Animals and Plants*. Methuen, London, UK.
- Flux, J.E.C., 1994. World distribution. In: Thompson, H.V., King, C.M. (Eds.), *The European Rabbit, the History and Biology of a Successful Colonizer*. Oxford University Press, Oxford, UK, pp. 8–21.
- Flux, J.E.C., Fullagar, P.J., 1992. World distribution of the rabbit *Oryctolagus cuniculus* on islands. *Mammal Review* 22, 151–205.
- Fuentes, E.R., Jaksic, F.M., Simonetti, J.A., 1983. European rabbits versus native rodents in central Chile: effects on shrub seedlings. *Oecologia* 58, 411–414.

- Fuentes, E.R., Otaiza, R.D., Alliende, M.C., Hoffmann, A., Poiani, A., 1984. Shrub clumps of the Chilean matorral vegetation: structure and possible maintenance mechanisms. *Oecologia* 62, 405–411.
- Fuentes, E.R., Hoffmann, A., Poiani, A., Alliende, M.C., 1986. Vegetation change in large clearings: patterns in the Chilean matorral. *Oecologia* 68, 358–366.
- Gajardo, R., 1994. *La Vegetación Natural de Chile*. Editorial Universitaria, Santiago, Chile.
- Grosholz, E.D., 2005. Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. *Proceedings of the National Academy of Sciences USA* 102, 1088–1091.
- Herrera, C.M., 1989. Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics in undisturbed Mediterranean habitats. *Oikos* 55, 250–262.
- Herrera, C.M., 1995. Plant–vertebrate seed dispersal systems in the Mediterranean: ecological, evolutionary, and historical determinants. *Annual Review of Ecology and Systematics* 26, 705–727.
- Hoffmann, A.J., Teillier, S., Fuentes, E.R., 1989. Fruit and seed characteristics of woody species in Mediterranean-type regions of Chile and California. *Revista Chilena de Historia Natural* 62, 43–60.
- Holmgren, M., 2002. Exotic herbivores as drivers of plant invasion and switch to ecosystem alternative states. *Biological Invasions* 4, 25–33.
- Homolka, M., 1988. Diet of the wild rabbit (*Oryctolagus cuniculus*) in an agrocoenosis. *Folia Zoologica* 37, 121–128.
- Howe, H.F., Smallwood, J., 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13, 201–228.
- Jaksic, F.M., 1998. Vertebrate invaders and their ecological impacts in Chile. *Biodiversity and Conservation* 7, 1427–1445.
- Jaksic, F.M., 2001. Spatiotemporal variation patterns of plants and animals in San Carlos de Apoquindo, central Chile. *Revista Chilena de Historia Natural* 74, 477–502.
- Jaksic, F.M., Fuentes, E.R., 1980. Why are native herbs in the Chilean matorral more abundant beneath bushes: microclimate or grazing? *Journal of Ecology* 68, 665–669.
- Jaksic, F.M., Fuentes, E.R., 1991. Ecology of a successful invader: the European rabbit in central Chile. In: Groves, R.H., di Castri, F. (Eds.), *Biogeography of Mediterranean Invasions*. Cambridge University Press, Cambridge, UK, pp. 273–283.
- Jaksic, F.M., Ostfeld, R.S., 1983. Numerical and behavioral estimates of predation upon rabbits in Mediterranean-type shrublands: a paradoxical case. *Revista Chilena de Historia Natural* 56, 39–49.
- Jaksic, F.M., Soriguer, C., 1981. Predation upon the European rabbit (*Oryctolagus cuniculus*) in Mediterranean habitats of Chile and Spain: a comparative analysis. *Journal of Animal Ecology* 50, 269–281.
- Jaksic, F.M., Fuentes, E.R., Yáñez, J.L., 1979. Spatial distribution of the Old World rabbit (*Oryctolagus cuniculus*) in central Chile. *Journal of Mammalogy* 60, 207–209.
- Jaksic, F.M., Schlatter, R.P., Yáñez, J.L., 1980. Feeding ecology of central Chilean foxes *Dusicyon culpaesus* and *Dusicyon griseus*. *Journal of Mammalogy* 61, 254–260.
- Jaksic, F.M., Iriarte, J.A., Jiménez, J.E., Martínez, D.R., 2002. Invaders without frontiers: cross-border invasions of exotic mammals. *Biological Invasions* 4, 157–173.
- Janzen, D.H., 1984. Dispersal of small seeds by big herbivores: the foliage is the fruit. *American Naturalist* 123, 338–353.
- Jimenez, H.E., Armesto, J.J., 1992. Importance of the soil seed bank of disturbed sites in Chilean matorral in early secondary succession. *Journal of Vegetation Science* 3, 579–586.
- Kruger, F.J., Breytenbach, G.J., Macdonald, I.A.W., Richardson, D.M., 1989. The characteristics of invaded Mediterranean climate regions. In: Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M., Williamson, M. (Eds.), *Biological Invasions: A Global Perspective*. Wiley, New York, USA, pp. 181–213.
- León-Lobos, P., Kalin-Arroyo, M.T., 1994. Germinación de semillas de *Lithrea caustica* (Mol.) H. et A. (Anacardiaceae) dispersadas por *Pseudalopex* sp. (Canidae) en el bosque esclerófilo de Chile central. *Revista Chilena de Historia Natural* 67, 59–64.
- Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K., Lavorel, S., 2003. Mechanisms underlying the impact of exotic plant invasions. *Philosophical Transactions of the Royal Society of London Series B* 270, 775–781.
- Malo, J.E., Suarez, F., 1995. Herbivorous mammals as seed dispersers in a Mediterranean dehesa. *Oecologia* 104, 246–255.
- Malo, J.E., Suarez, F., 1997. Dispersal mechanism and transcontinental naturalization proneness among Mediterranean herbaceous species. *Journal of Biogeography* 24, 391–394.
- Malo, J.E., Jiménez, B., Suarez, F., 2000. Herbivore dunging and endozoochorous seed deposition in a Mediterranean dehesa. *Journal of Range Management* 53, 322–328.
- Maron, J.L., Vilà, M., 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* 95, 361–373.
- McKey, D., 1975. The ecology of coevolved seed dispersal systems. In: Gilbert, L.E., Raven, P. (Eds.), *Coevolution of Animals and Plants*. University of Texas Press, Austin, TX, pp. 159–191.
- Merton, D., Climo, G., Laboudallon, V., Robert, S., Mander, C., 2001. Alien mammal eradication and quarantine on inhabited islands in the Seychelles. In: Veitch, C.R., Clout, M.N. (Eds.), *Turning the Tide: The Eradication of Invasive Species*. IUCN, SSC, Invasive Species Specialist Group, IUCN, Gland, Switzerland and Cambridge, UK, pp. 182–198.
- Myers, J.A., Vellend, M., Gardescu, S., Marks, P.L., 2004. Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia* 139, 35–44.
- Olf, H., Ritchie, M.E., 1998. Effect of herbivores on grassland plant diversity. *Trends in Ecology and Evolution* 13, 261–265.
- Pakeman, R.J., Engelen, J., Attwood, J.P., 1999. Rabbit endozoochory and seedbank build-up in an acidic grassland. *Plant Ecology* 145, 83–90.
- Pakeman, R.J., Engelen, J., Attwood, J.P., 2002. Ecological correlates of endozoochory by herbivores. *Functional Ecology* 16, 296–304.

- Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E., Goldwasser, L., 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1, 3–19.
- Poulsen, J.R., Clark, C.J., Connor, E.F., Smith, T.B., 2002. Differential resource use by primates and hornbills: implication for seed dispersal. *Ecology* 83, 228–240.
- Reid, N., 1989. Dispersal of mistletoes by honeyeaters and flowerpeckers: components of seed dispersal quality. *Ecology* 70, 137–145.
- Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J., Rejmánek, M., 2000. Plant invasions—the role of mutualisms. *Biological Reviews* 75, 65–93.
- Rodríguez, R., Matthei, O., Quezada, M., 1993. Flora Arbórea de Chile. Editorial de la Universidad de Concepción, Concepción, Chile.
- Rundel, P.W., 1981. The matorral zone of central Chile. In: di Castri, F., Goodall, D.W., Specht, R.L. (Eds.), *Mediterranean Type Shrublands*. Elsevier Scientific Publishers, Amsterdam, The Netherlands, pp. 175–201.
- Selkirk, P.M., Costin, A.B., Seppelt, R.D., Scott, J.J., 1983. Rabbits, vegetation and erosion on Macquarie Island. *Proceedings of the Linnaean Society of N.S.W.* 106, 337–346.
- Simberloff, D., Von Holle, M., 1999. Synergistic interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1, 21–32.
- Sokal, R.R., Rohlf, F.J., 1994. *Biometry: The Principles and Practice of Statistics in Biological Research*, third ed. Freeman, New York, NY.
- Taylor, R.H., 1968. Introduced mammals and islands: priorities for conservation and research. *Proceedings of the New Zealand Ecological Society* 15, 61–67.
- Thompson, H., King, C., 1994. *The European Rabbit: The History and Biology of a Successful Colonizer*. Oxford University Press, Oxford, UK.
- Vellend, M., Myers, J.A., Gardescu, S., Marks, P.L., 2003. Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. *Ecology* 84, 1067–1072.
- Verdú, M., García-Fayos, P., 2002. Ecología reproductiva de *Pistacia lentiscus* L. (Anacardiaceae): un anacronismo evolutivo en el matorral mediterráneo. *Revista Chilena de Historia Natural* 75, 57–65.
- Wang, B.J., Smith, T.B., 2002. Closing the seed dispersal loop. *Trends in Ecology and Evolution* 17, 379–385.
- Welch, D., 1985. Studies in the grazing of heather moorland in north-east Scotland. IV. Seed dispersal and plant establishment in dung. *Journal of Applied Ecology* 22, 461–472.
- Wilcove, D.S., Rothstein, D., Bubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. *BioScience* 48, 607–615.
- Williamson, M., 1996. *Biological Invasions*. Chapman & Hall, London, UK.
- Zavaleta, E.S., Hobbs, R.J., Money, H.A., 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution* 16, 454–459.