

Avian gut-passage effects on seed germination of shrubland species in Mediterranean central Chile

Sharon Reid · Juan J. Armesto

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Abstract Effects of avian gut-passage on seed germination are important to assess the effectiveness of frugivores in woodland regeneration, particularly in biodiversity hotspots that have a high incidence of avian frugivory. We examined the effect of avian gut-passage on seed germination in contrast to seeds that remain uneaten in five shrub species in Mediterranean central Chile and sought to determine the physiological mechanism(s) by which seed germinability is modified. Germination assays were conducted in a glasshouse for five common shrub species of the sub-Andean matorral: *Azara dentata* (Flacourtiaceae), *Schinus polygamus* and *Schinus molle* (Anacardiaceae), *Cestrum parqui* (Solanaceae), and *Maytenus boaria* (Celastraceae). We estimated germinability (final percent germination), dormancy length (time from sowing to first germination), mean length of dormancy of all germinated seeds, and contrasted germination rates of defecated versus manually extracted and pulp-enclosed seeds. Avian gut-passage increased seed germinability in four of the five shrub species studied—primarily through deinhibition

via pulp removal. Minimum dormancy length was not modified by avian gut-passage for *A. dentata*, but was significantly shorter for *S. molle* and *C. parqui*. Mean dormancy length was significantly shorter in gut-passed seeds of *A. dentata*, *S. molle* and *M. boaria*. Avian gut-passage greatly enhanced the seed germination rates of three species, *A. dentata*, *S. molle* and *C. parqui*. We conclude that the positive effects of birds on seed germination facilitate the regeneration of sub-Andean shrublands, and that bird declines due to landscape change may impair recovery rates of successional or restored areas due to dispersal limitation.

Keywords Deinhibition effect · Germinability · Scarification effect · Seed dormancy · Dispersal limitation

Introduction

Seed dispersal may limit or facilitate plant regeneration under different scenarios of land cover and climate change. Studies of animal seed dispersal should evaluate three types of dispersal-related processes: processes that take place on the source plant (e.g., fruit selection, handling, and removal patterns of frugivores), processes during relocation (e.g., gut-passage time of seeds, rate of seed survival inside the frugivore), and processes at the destination (e.g., number of seeds in droppings, conditions at the deposition site, and habitats where seeds are deposited).

S. Reid (✉) · J. J. Armesto
Center for Advanced Studies in Ecology and Biodiversity (CASEB), Departamento de Ecología, Pontificia Universidad Católica de Chile, Alameda 340, Casilla 114-D, Santiago 6513677, Chile
e-mail: sreid@bio.puc.cl

S. Reid · J. J. Armesto
Institute of Ecology and Biodiversity (IEB), Casilla 653, Santiago, Chile

The contribution of these sets of processes to successful seed dispersal, seed deposition at sites where seeds can germinate and seedlings can establish successfully, depends largely on the behaviour and physiology of seed vectors and on the landscape structure where the animals move (Nathan 2006; Russo et al. 2006; Jordano et al. 2007; Skarpaas et al. 2007).

Although assessing the effects of avian gut-passage on seed germination is an essential component of the research protocol for analysing the effectiveness of frugivores as seed dispersers in any landscape context, this assessment is often omitted. A review of post-dispersal seed germination assays shows that frugivores can significantly enhance seed germination, but only for about half of the species that have been tested (Traveset 1998). Enhanced seed germination can occur either through enhanced seed germinability (the percentage of germinated seeds at the end of the growing season) or the rate of seed germination (Schupp 1993; Traveset 1998; Traveset and Verdú 2002; Traveset et al. 2007). However, in many cases seed germination remains unchanged or may even decrease following gut-passage.

Frugivores can enhance seed germination by three mechanisms: (1) through mechanical or chemical scarification (degradation) of the impermeable seed coat or endocarp (scarification effect; Barnea et al. 1990; Traveset 1998); (2) through the removal of the pulp that contains chemicals that can block germination pathways (deinhibition effect; Cipollini and Levey 1997; Samuels and Levey 2005); and (3) through the effect of the faecal material surrounding the seed (fertilization effect; Traveset and Verdú 2002). Few studies have tested the occurrence of scarification, deinhibition and fertilization mechanisms in field or laboratory assays (but see Kelly et al. 2004; Samuels and Levey 2005; Linnebjerg et al. 2009). In particular, only 22% of 99 studies reviewed by Samuels and Levey (2005) simultaneously compared the germinability of gut-passed seeds to both manually extracted seeds and seeds within intact fruits.

In the Mediterranean-type shrubland of central Chile (Chilean matorral hereafter), where humans have greatly changed the distribution and cover of woodland vegetation over large areas of the landscape, regeneration of woody species in open areas is likely limited by seed inputs, in contrast to other Mediterranean areas in North America, Europe and Australia, because soil or aerial seed banks of woody

species are extremely poor or entirely absent (Fuentes et al. 1984; Jiménez and Armesto 1992; Hoffmann and Armesto 1995; Figueroa et al. 2004). In addition, the matorral presents a high incidence of fleshy-fruited, avian-dispersed woody species (Hoffmann and Armesto 1995), which contrasts with the predominant seed dispersal modes in other Mediterranean areas of the world, where fire adaptations such as on-plant seed storage (i.e., serotinous species), fire-stimulated seed dispersal and seed germination (e.g., the California chaparral, Australian mallee and South African fynbos) or ant-seed dispersal (e.g., the Australian mallee) occur in a high proportion of the flora (Keeley 1995; Figueroa et al. 2009). Seed germination of woody species is not responsive to fire or smoke stimulation in central Chile (Hoffmann and Armesto 1995).

Despite the high dependence of woody species regeneration on avian frugivory, information about the ecological role of birds for the regeneration dynamics of the Chilean matorral remains anecdotal, and we lack precise information about the actual seed dispersers, their behaviours, and their effects on seed inputs and seed germination (Hoffmann and Armesto 1995). In this historical and ecological context, we hypothesize that the potential for regeneration of Chilean matorral shrubs may be limited proximally by the arrival of viable seeds from source areas, which in turn depend on the feeding and behavioural patterns of frugivores. Given that a mean of 14 plant species, i.e., 34.3% (in the range 10.5–53.1%) of the total woody flora in a gradient from dry to wet sites bear fleshy fruits dispersed primarily by birds (Hoffmann et al. 1989; Hoffmann and Armesto 1995), we evaluate here the effect of avian gut-passage on seed germination of five common woody species of sub-Andean shrublands, whose fruits are consumed by a few species of birds in central Chile (Hoffmann and Armesto 1995; Reid 2008). These shrub species conform 90% of the seed contents found in bird droppings and are frequent on the mountain slopes surrounding the large city of Santiago, where vegetation is slowly recovering from nearly a century-old large-scale effects of livestock grazing, anthropogenic fire and firewood extraction (Reid 2008). We compared the responses of bird-defecated seeds, to seeds manually extracted from fruits and seeds surrounded by intact pulp. We addressed the following specific questions: what are the effects of avian

gut-passage on seed germination responses, including seed germinability and time to germination, and what are the possible physiological mechanism(s) by which seed germinability can be modified by the avian seed vector. We specifically tested for the effects of scarification and deinhibition, because avian-ingested seeds in our study were sowed without faecal material. We expect that an understanding of dispersal-related process, focusing on seed survival during relocation, will shed light on the effectiveness of avian frugivores to facilitate the recovery of shrublands in heavily impacted anthropogenic landscapes. Understanding the mechanisms that limit or facilitate natural regeneration of plants in this Mediterranean area can apply to other regions where avian seed dispersal can also be limiting recruitment (e.g., European maquis and the California chaparral). Dispersal limitation can be a serious problem for succession and restoration in a number of biodiversity hotspots, which are globally threatened by changes in land use and disrupted biotic interactions (Arroyo et al. 1999; Myers et al. 2000; Sala et al. 2000).

Methods

Study area

Collection of seeds for germination assays were conducted in the Estación de Investigaciones Ecológicas Mediterráneas (EDIEM hereafter), which

includes 835-ha of land in the outskirts of Santiago (33°23' S, 70°31' W). The vegetation is classified as evergreen sclerophyllous woodland, and lies on the Andean foothills, 20 km east of Santiago, between 1,050 and 1,915 m. Climate is summer-dry Mediterranean with a mean yearly rainfall of 433.6 mm and a mean air temperature of 14.8°C (EDIEM, 4 year records). See Jaksic (2001) for a full description of this site.

Species studied

We collected seeds of five bird-dispersed woody species, *A. dentata* (Flacourtiaceae), *S. polygamus*, *S. molle* (Anacardiaceae), *C. parqui* (Solanaceae) and *M. boaria* (Celastraceae; Table 1). Percent ground cover of each species was estimated as the projected canopy cover intercepting ten 90-m linear transects, five on a south-facing slope and five on a plain located 150 m away to incorporate local differences in vegetation cover. *A. dentata* had the highest ground cover of the group in the study site, and was more abundant on alluvial fans where edaphic humidity is greater (Jaksic 2001). *M. boaria* and *S. polygamus* followed in cover; the former has been described as a late-successional colonizer by Armesto and Pickett (1985). *C. parqui* was a relatively uncommon species in the area, often found in disturbed sites (e.g., clearings, near roads). *S. molle* was not naturally present in this shrubland, but it has been locally planted as ornamental in the adjacent sports club, and

Table 1 List of species studied in the Mediterranean shrubland of central Chile, their families, growth forms, fruiting periods, fruit traits, mean ground cover and total number of seeds used for each treatment

	Shrub species				
	<i>A. dentata</i>	<i>S. polygamus</i>	<i>S. molle</i>	<i>C. parqui</i>	<i>M. boaria</i>
Family	Flacourtiaceae	Anacardiaceae	Anacardiaceae	Solanaceae	Celastraceae
Growth form	Shrub	Shrub	Tree	Shrub	Tree
Fruiting period	Jan–Jul	Jan–Aug	Feb–May	Jan–Sep	Feb–May
Fruit type	Berry	Drupe	Drupe	Berry	Dehiscent capsule containing two arillated seeds
Fruit colour	Orange	Purple-black	Pale pink	Purple-black	Dark orange aril
Fruit diameter (mm)	4–5	5	5–9	10	5–7
Species cover (%)	2.9	1.9	0	0.1	1.7
Mean number of seeds per fruit	4 ± 2	1	1	4 ± 1.5	2
Number of bird defecated seeds	90	100	40	20	8

it has likely expanded its population via bird-seed dispersal in recent years (Hoffmann 1998). Information on the identity of frugivores in central Chile is limited, but we were able to determine that fruits of *A. dentata*, *C. parqui*, *S. polygamus* and *S. molle* were primarily consumed by *Turdus falcklandii* (Turdidae) and by the summer migrant *Elaenia albiceps* (Tyrannidae), while those of *C. parqui* and *S. polygamus* were also consumed by *Mimus thenca* (Mimidae) and *Zonotrichia capensis* (Emberizidae); finally, fruits of *S. polygamus* were also consumed by the woodpecker *Colaptes pitius* (Picidae; Reid 2008). Arillated seeds of *M. boaria* were consumed mainly by the winter migrant, *Colorhamphus parvirostris*, and by *Xolmis pyrope* (both Tyrannidae; Hoffmann and Armesto 1995; Reid 2008).

Collection of bird-dispersed seeds

During the austral summer of 2006 (January–March), we collected as many bird droppings containing shrub seeds as possible within the matorral of the EDIEM. Immediately after collection, seeds were kept separated by species in paper bags, under dark and dry conditions until they were analysed. We were unable to distinguish droppings from different bird species, and because of our fruit removal observations, we assumed that they derived from the bird species cited above (Reid 2008). We commonly found shrub seeds in the bird droppings, with exception of *M. boaria* that was included because many seeds were obtained directly from a mist-net capture of *C. parvirostris* in a parallel study. This was the first record of consumption and defecation of intact seeds by this bird species. Accordingly, germination assays allowed us to assess the role of *C. parvirostris* as an effective seed disperser. During the study period, we also collected fresh fruits from a minimum of five individuals of each of the five shrub species found in bird droppings. We manually removed the pulp from a number of seeds corresponding to the number of seeds extracted from bird droppings and stored the seeds under dark and dry conditions. The remaining intact fruits were refrigerated at 4°C until the date of sowing.

Experimental design

Seed germination assays were conducted in the glasshouse of the Ecology Department of the

Pontificia Universidad Católica de Chile in Santiago. Glasshouse conditions were set for a spring ratio of 14 h light/10 h darkness. Light intensities were from 350 to 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ from a metal halide light measured at the outer surface of containers. Temperature ranged from 16 to 28°C during the assays. For each shrub species, treatments were seeds collected from bird droppings (ingested seeds hereafter), seeds manually removed from the pulp by hand (extracted seeds hereafter), and seeds sowed with the pulp (intact fruits). The numbers of seeds collected from bird droppings set the number of replicates per shrub species for each treatment (Table 1). Seeds were placed on filter paper in Petri dishes, 9-cm diameter, and watered every 2–3 days with distilled water. We placed 10 seeds per species in each Petri dish, except for *M. boaria*, for which only eight seeds were obtained from droppings. We tallied the number of seeds germinated every 3 days, by recording the emergence of the radicle during 3 months (108 days in total) in the austral winter and spring (July–October, 2006). A total of 774 seeds were tested overall. As germination responses, we assessed (1) germinability (the final percentage of sown seeds germinated after 3 months); (2) the minimum length of seed dormancy (T_0 , defined as the number of days elapsed from sowing until the first radicle emerged; Traveset et al. 2001); (3) mean length of seed dormancy (MLD, defined as the mean number of days since sowing to germination of all germinated seeds, Garwood 1983) and (4) germination rate (defined as the number of seeds germinated per time interval).

Data analyses

For germinability, data were arcsine-transformed to normalize germination percentages (Traveset et al. 2001) and treatments were examined by a one-way ANOVA with further comparisons made using Tukey's post-hoc tests. For *A. dentata*, normality was not met so a Kruskal–Wallis test was performed, and Mann–Whitney tests were used to make paired comparisons. For the minimum length of seed dormancy (T_0) for *S. molle* and *A. dentata* (the latter previously log-transformed), T_0 was compared among treatments by an ANOVA and Tukey's post-hoc test. A non-parametric Mann–Whitney test was used for *C. parqui*. In order to compare MLDs, the treatment with the lowest number of germinated

seeds set the sample sizes for dormancy values to have a balanced ANOVA; then we randomly drew the replicates for each treatment. MLD was compared using a Kruskal–Wallis test for *S. molle*, and paired comparisons among treatments were made with the Mann–Whitney test for this species and *A. dentata* and *M. boaria* (for the latter two species, MLD was only compared between ingested and extracted seeds). MLD was not analysed for *C. parqui* because of limited sample sizes. Germination rates were compared among treatments for each species using a repeated-measures analysis of variance (RMANOVA). In addition, Kaplan–Meier survival analysis was used to assess differences in cumulative seed germination curves among treatments. Post-hoc pairwise multiple comparisons were performed with the Holm–Sidak method (HS, significance level ≤ 0.05). All tests were performed using Systat V. 8.0 and SigmaStat 3.1 software (SPSS Inc.).

Results

Germinability

For *A. dentata*, there was a significant treatment effect (Kruskal–Wallis = 18.33, $P < 0.001$), specifically between seeds sowed with pulp, in contrast to ingested (Mann–Whitney U -test: $Z = 3.58$, $P < 0.001$) and manually extracted seeds (Mann–Whitney U -test: $Z = 3.58$, $P < 0.001$), but the total germination did not differ between ingested and extracted seeds (Mann–Whitney U -test: $Z = 0.09$, $P = 0.93$; Table 2; Fig. 1a). During the 3 months of the experiment, no seeds sowed with pulp germinated (Fig. 1a). For *S. molle*, germinability was significantly higher for bird-ingested seeds than for seeds sowed with pulp (ANOVA $F_{2,9} = 4.94$, $P = 0.04$; Tukey's test, $P = 0.03$; Fig. 1b). For *C. parqui*, germinability differed significantly among all three treatments (ANOVA $F_{2,3} = 10.25$, $P = 0.05$). In particular, final percent germination was significantly greater for bird-ingested than for manually extracted seeds (Tukey, $P = 0.04$; Table 2; Fig. 1c). In *M. boaria*, germinability was equal for ingested and extracted seeds (seven seeds germinated out of eight, 85% germinability) and half the seeds sowed with the pulp germinated (Fig. 1d). In contrast, only one out of 100 seeds of *S. polygamus* germinated in each of

the ingested and the intact fruit treatments, and no extracted seeds germinated (Table 2).

Length of seed dormancy (MLD and T_0)

T_0 did not vary between ingested and manually extracted *A. dentata* seeds ($F_{1,16} = 3.42$, $P = 0.08$), but MLD was significantly shorter in the sample of bird-ingested seeds (Mann–Whitney U -test: $Z = 4.13$, $P = 0.04$; Table 2). In the case of seeds of *S. molle*, T_0 varied marginally significantly among treatments ($F_{2,9} = 3.8$, $P = 0.06$); and a Tukey's test showed that bird-ingested seeds germinated faster than those sowed with pulp (Tukey, $P = 0.05$). The MLD differed significantly among sowing treatments (Kruskal–Wallis = 10.95, $P = 0.004$); specifically between ingested and manually extracted seeds, and between manually extracted and seeds with intact pulp (Mann–Whitney U -test: $Z = 3.84$, $P = 0.05$ and $Z = 11.21$, $P = 0.001$, respectively; Table 2). Statistical comparisons of T_0 in the case of *C. parqui* were only possible between ingested seeds and seeds within intact fruits (only one seed germinated in the manually extracted seed treatment). T_0 was significantly longer for seeds sowed with pulp (Mann–Whitney U -test: $Z = -2.31$, $P = 0.02$; Table 2). In *M. boaria*, MLD was 24 days shorter for bird-ingested than for manually extracted seeds (Mann–Whitney U -test: $Z = 7.6$, $P = 0.01$; Table 2).

Germination rates

The seed germination rate of *A. dentata* differed significantly among treatments as no seeds germinated inside intact fruits (RMANOVA $F_{2,24} = 9.47$, $P = 0.001$; Fig. 1a), while higher germination rates for ingested and extracted seeds did not differ from each other (RMANOVA $F_{1,16} = 1.22$, $P = 0.28$ and HS, $P = 0.49$).

In the case of *S. molle*, seed germination rate varied significantly among treatments (RMANOVA $F_{2,9} = 5.29$, $P = 0.03$; Fig. 1b). Paired comparisons of seed germination rates between ingested and manually extracted seeds of *S. molle* showed no significant difference (RMANOVA $F_{1,6} = 2.66$, $P = 0.15$). However, the difference between ingested and seeds sowed with pulp indicated a significant effect of gut-passage, which enhanced seed germination rate (RMANOVA $F_{1,6} = 18.91$, $P = 0.01$).

Table 2 Percent germinability, minimum dormancy length (T_0) and mean length of the dormancy period (MLD) in days for each species

	Treatments		
	Ingested	Manually extracted	Intact fruit
<i>A. dentata</i>			
Germinability (%)	26.67 $\pm$ 16.58* (9)	24.44 $\pm$ 12.36** (9)	0
T_0	39 $\pm$ 7.65 (9)	48 $\pm$ 12.19 (9)	– ^b
MLD	45.75 $\pm$ 10.55****	52.77 $\pm$ 10.9	– ^b
<i>S. polygamus</i>			
Germinability (%)	1 $\pm$ 3.16 (10)	0 (10)	1 $\pm$ 3.16 (10)
T_0	12 (1 ^a)	– ^b	18 (1 ^a)
MLD	–	– ^b	–
<i>S. molle</i>			
Germinability (%)	72.5 $\pm$ 9.57*** (4)	42.5 $\pm$ 25 (4)	27.5 $\pm$ 23.63 (4)
T_0	10.5 $\pm$ 1.73*** (4)	12 $\pm$ 2.45 (4)	14.25 $\pm$ 1.5 (4)
MLD	14.73 $\pm$ 4.92****	11.73 $\pm$ 1.62**	17.18 $\pm$ 5.21
<i>C. parqui</i>			
Germinability (%)	95 $\pm$ 7.07**** (2)	5 $\pm$ 7.07 (2)	15.56 $\pm$ 0 (2)
T_0	7.5 $\pm$ 2.12*** (2)	15 (1 ^a)	12 $\pm$ 0 (2)
<i>M. boaria</i>			
Germinability (%)	87.5	87.5	50
T_0	15	42	39
MLD	41.14 $\pm$ 17.12****	65.14 $\pm$ 11.45	54.75 $\pm$ 10.78

These parameters are compared among three treatments related to seed dispersal: bird-ingested seeds (collected from bird droppings), extracted seeds (seeds extracted manually from the pulp) and seeds within intact fruits (fruits collected directly from the plants). Data are means $\pm$ one SD; number of Petri dishes in parentheses. Each Petri dish contained 10 seeds

^a T_0 calculated using fewer numbers of Petri dishes, as no seeds germinated in the other Petri dishes for these treatments

^b Not calculated because of zero germination

* $P < 0.001$ (between ingested and intact fruit treatments); ** $P < 0.001$ (between extracted and intact fruit); *** $P \leq 0.05$ (between ingested and intact fruit); **** $P \leq 0.05$ (between ingested and extracted seeds)

Cumulative germination was significantly higher in gut-passed seeds compared to seeds inside intact fruits (HS, $P = 0.01$).

In *C. parqui*, germination rate differed significantly among treatments (RMANOVA $F_{2,3} = 97.55$, $P < 0.01$; Fig. 1c). Paired comparisons showed that the germination rate of gut-passed seeds was significantly faster than manually extracted and pulp-enclosed seeds (RMANOVA $F_{1,2} = 110.45$, $P = 0.01$ and $F_{1,2} = 108.97$, $P = 0.01$, respectively). Cumulative germination was significantly higher in gut-passed seeds compared to both manually extracted and pulp-enclosed seeds (HS, $P = 0.01$ and HS, $P = 0.02$, respectively).

Finally, for *M. boaria*, there was a significant difference between the cumulative seed germination

curves for gut-passed and intact fruits (GB = 8.88, $df = 2$, $P = 0.01$). In particular, gut-passed seeds had a significantly higher cumulative germination percentage than pulp-enclosed seeds (HS, $P = 0.02$; Fig. 1d).

Discussion

This study identifies for the first time the physiological effects of avian frugivory on seed germination patterns in a southern hemisphere Mediterranean shrubland, where birds are major seed vectors. Plant–frugivore interactions strongly influence the patterns of succession and recovery from disturbance in these areas (Armesto and Pickett 1985; Armesto et al.

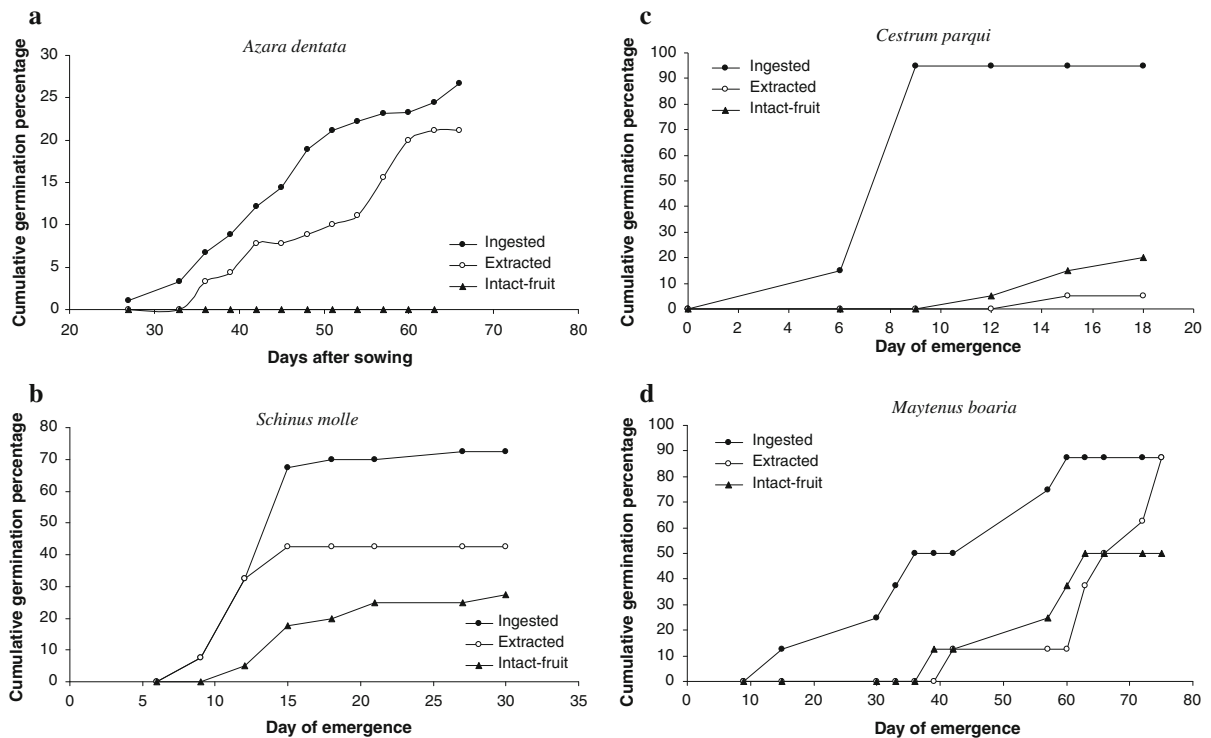


Fig. 1 Cumulative seed germination percentages for each seed manipulation treatment, for *A. dentata* (a), *S. molle* (b), *C. parqui* (c) and *M. boaria* (d)

1995). As bird species disperse a large number of seeds of shrub species, and, as shown here, they can enhance seed germination rates, it seems likely that seed input may be limiting succession over extensive areas of the Chilean matorral where vegetation and animal communities have been disrupted by fire and grazing (J. Armesto, unpubl. results). Further research on species-specific effects of different bird species on seed germination are urgently needed to better understand the functional role of avian frugivores for the regeneration and maintenance of plant diversity in this system.

Compared to seeds sowed with pulp or those manually extracted from fruits, seeds ingested by birds significantly increased their germinability for four of the five Mediterranean shrub species that have fleshy fruits commonly consumed by birds in the sub-Andean landscape. Our results suggest that pulp removal after ingestion (by the frugivore) strongly enhances seed germination through eliminating chemical inhibitors that may be present in the fruit pulp. These results support the conclusion reached by Robertson et al. (2006), in a review of 51 plant

species from 28 families, which have seeds internally dispersed by birds, indicating that deinhibition effects were significantly larger than scarification effects.

While comparing among the four shrub species studied here, we find that the highest enhancement effect of pulp removal was detected in *S. molle*. However, in this particular case, we were unable to identify the mechanism responsible for germination enhancement because significantly increased germinability was found only for ingested seeds compared to seeds sowed with pulp. The lack of significant differences between ingested and manually extracted seeds led us to reject the scarification effect, and because no significant differences were found between manually extracted seeds and those sowed with pulp, there was no clear evidence for a deinhibition effect. Nevertheless, significantly higher germinability of gut-passed seeds compared to seeds sowed with pulp allows an assessment of the combined effect of both processes (Traveset et al. 2007). This species, which has been planted as ornamental in many neighbouring gardens, can likely expand its population via bird-seed dispersal to preexisting perches in the matorral (e.g.,

trees and shrubs) which are favourable for germination. Naturalization and invasion of *S. molle* in other Mediterranean areas has been observed in California, South Africa and Australia (Howard and Minnich 1989; Randall 2002; Iponga et al. 2009).

In the case of *A. dentata*, we must reject scarification and support deinhibition effect, because of higher germinability of both ingested and manually extracted seeds compared to seeds within intact fruits. The fact that seeds within intact fruits did not germinate at all suggests that *A. dentata* is more dependent than the other shrub species on avian frugivory to complete its reproductive cycle. Scarification effect of bird ingestion is strongly suggested by the enhanced germinability of *C. parqui*, as large differences were observed between gut-passed and manually extracted seeds, while no difference was observed between manually extracted and seeds surrounded by intact pulp. In the case of *M. boaria*, deinhibition and scarification may explain the higher overall percentage of germination for both ingested and manually extracted seeds (Figueroa and Jaksic 2004, and references therein). Finally, as we did not have a control for seed viability previous to sowing, it is possible that low seed germination obtained for some treatments in the cases of *A. dentata*, *S. polygamus* and *C. parqui* was the result of secondary dormancy or non-viable seeds. Lack of seed germination recorded in *S. polygamus* may be due to its low seed viability, because differences in seed viability from 3 to 80% have been documented for different seed lots of this species (A. Sandoval, unpubl. results).

The effect of avian gut-passage on the mean length of seed dormancy (MLD) varied among the four shrub species studied, but overall estimates of MLD differed from the results for T_0 . Significant differences in MLD were observed between ingested and extracted *A. dentata* seeds (but undetected for T_0) and between manually extracted *S. molle* seeds and both ingested and pulp-enclosed seeds. In the case of *A. dentata*, a larger sample size allows us to use MLD as a germination response variable, with more statistical power than T_0 . In the case of the tree *M. boaria*, although gut-passage of seeds ingested by *Colorhamphus parvirostris* significantly shortened the MLD, we could not directly quantify the effect of ingestion. Finally, we recommend MLD (*sensu* Garwood 1983) as a suitable index for assessing the effect of gut-passage on the breaking of seed

dormancy, especially when sample sizes limit comparisons.

Enhanced seed germinability can be positively related to plant fitness, as avian ingestion is necessary for the completion of the plant reproductive cycle and can potentially increase seedling recruitment (Traveset et al. 2007). This may be the case for *A. dentata* whose seeds did not germinate when enclosed by the fruit pulp, suggesting strong dependance on avian frugivory to recruit in vegetated or open areas.

The possible advantages of faster germination or shorter dormancy periods for shrub seeds under Mediterranean climate are not fully understood. An advantage of faster seed germination is that dispersed seeds have a shorter exposure to local seed predators (Traveset et al. 2001). In addition, seedlings emerging rapidly in early spring may develop deeper root systems than late emerging seedlings in the field. This can make rapidly emerging seedlings more resistant to subsequent summer drought, overall exhibiting higher survival rates (Paulsen and Högstedt 2002). It can also be suggested that fruit consumption by birds adds temporal heterogeneity to seed germination responses, by enhancing germination rates and shortening seed dormancy throughout the entire ripe-fruit period, which may last from 5 to 9 months for these shrub species (Jaksic 2001). With the added observation that many seeds remain undispersed and fall to the ground within the pulp, accelerated germination and enhanced root growth can ensure that at least some seedlings will survive the lack of summer rainfall characteristic of most Mediterranean shrublands. The advantage of increased temporal germination heterogeneity in variable environments is spreading the risk of seed and seedling mortality over time (Izhaki and Safriel 1990).

Seeds that we collected from droppings most likely came from more than one bird species. We recorded that fruits of *A. dentata*, *C. parqui* and *S. molle* were consumed by two bird species, *Turdus falcklandii* and *Elaenia albiceps*, while fruits of *C. parqui* were also consumed by two other bird species, *Mimus thenca* and *Zonotrichia capensis*. Different frugivores distribute seeds over widely different areas and possibly habitats, and also affect seed germinability differentially due to differences in gut-retention times and/or by mixing other food items along with the ingested seeds (Izhaki and Safriel 1990; Barnea et al. 1991; Traveset et al. 2001, 2007).

Differences in frugivore behaviour and physiology combined with the intrinsic variability of seed and fruit traits (e.g., pulp chemical composition, seed age, seed size, coat thickness, etc.) contribute to broaden the timing of seed germination and the spatial distribution of seeds within and across plant communities.

Enhanced seed germination after gut-passage does not, by itself, guarantee the effectiveness of particular bird species as seed dispersers (*sensu* Schupp 1993); nevertheless, we showed that avian frugivores in this Mediterranean ecosystem did not harm seeds after gut-passage and tend to speed up germination. A high proportion (>60%) of seeds consumed by avian frugivores are transported to favourable sites for recruitment in the human-degraded landscape, particularly dropped under tall shrubs that keep moisture longer in the soil (Reid 2008). Because the majority of shrub and tree species in the Chilean matorral have fleshy fruits, we predict that the natural recovery of woodlands from disturbance by fire and grazing will be at greater risk than in other Mediterranean areas (e.g., fynbos and mallee), as changes in cover affect bird species composition and abundances (Estades 2004) as well as plant–bird interactions (Reid and Armesto 2010).

In sum, in this Mediterranean shrubland, we documented that avian gut-passage increased seed germinability, mainly through removal of pulp inhibitors, thus showing that regeneration of woodland species is highly dependent on bird consumption of fruits and subsequent behaviour of avian frugivores. As human impacts have greatly changed the extent of vegetation cover and floristic composition of Mediterranean shrublands, and these in turn may have significant effects on bird populations and their interactions, the recovery of shrub cover following large disturbances may be seriously impaired. Dispersal limitation may be strong as seed banks are generally lacking (Jiménez and Armesto 1992) and seedling establishment depends largely on annual seed input via bird dispersal. We suggest that future research should focus on the specific effects of major frugivores on the spatial distribution and germination of shrub seeds. Likewise, germination assays with non-ingested fruits in the field can help determine how pericarp decay may favour or deter germinability, and how recruitment would be affected by the local extinction or decline of major frugivores.

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References

- Armesto JJ, Pickett STA (1985) A mechanistic approach to the study of succession in the Chilean matorral. *Rev Chil Hist Nat* 58:9–17
- Armesto JJ, Vidiella PE, Jiménez HE (1995) Evaluating causes and mechanisms of succession in the Mediterranean regions in Chile and California. In: Arroyo MTK, Zedler PH, Fox MD (eds) *Ecology and biogeography of Mediterranean ecosystems in Chile, California and Australia*. Springer-Verlag, New York, USA, pp 418–433
- Arroyo MTK, Rozzi R, Simonetti JA, Marquet PA, Salaberry M (1999) Central Chile. In: Mittermeier R, Myers N, Goettsch-Mittermeier C (eds) *Earth's biologically richest and most endangered terrestrial ecoregions*. Cemex, México, pp 161–171
- Barnea A, Yom-Tov Y, Friedman J (1990) Differential germination of two closely related species of *Solanum* in response to bird ingestion. *Oikos* 57:222–228
- Barnea A, Yom-Tov Y, Friedman J (1991) Does ingestion by birds affect seed germination? *Funct Ecol* 5:394–402
- Cipollini ML, Levey DJ (1997) Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *Am Nat* 150:346–372
- Estades CF (2004) Estrategia nacional para la conservación de las aves. Unión de Ornitólogos de Chile y Programa Multidisciplinario de Estudios en Biodiversidad de la Universidad de Chile
- Figueroa JA, Jaksic FM (2004) Latencia y banco de semillas en plantas de la región mediterránea de Chile central. *Rev Chil Hist Nat* 77:201–215
- Figueroa JA, Teillier S, Jaksic FM (2004) Composition, size and dynamics of the seed bank in a Mediterranean shrubland of Chile. *Austral Ecol* 29:574–584
- Figueroa JA, Cavieres LA, Gómez-González S, Molina Montenegro M, Jaksic F (2009) Do heat and smoke increase emergence of exotic and native plants in the matorral of central Chile? *Acta Oecol* 35:335–340
- Fuentes ER, Otaíza RD, Alliende MC, Hoffmann AJ, Poiani A (1984) Shrub clumps of the Chilean matorral vegetation: structure and possible maintenance mechanisms. *Oecologia* 62:405–411
- Garwood NC (1983) Seed germination in a seasonal tropical forest in Panama: a community study. *Ecol Monogr* 53:159–181

- Hoffmann A (1998) El árbol urbano de Chile, 3rd edn. Fundación Claudio Gay, Santiago, Chile
- Hoffmann AJ, Armesto JJ (1995) Modes of seed dispersal in the Mediterranean regions in Chile, California and Australia. In: Arroyo MTK, Zedler PH, Fox MD (eds) Ecology and biogeography of Mediterranean ecosystems in Chile, California and Australia. Springer-Verlag, New York, USA, pp 289–310
- Hoffmann AJ, Teillier S, Fuentes ER (1989) Fruit and seed characteristics of woody species in Mediterranean-type regions of Chile and California. *Rev Chil Hist Nat* 62: 43–60
- Howard LF, Minnich RA (1989) The introduction and naturalization of *Schinus molle* (pepper tree) in Riverside, California. *Landsc Urban Plan* 18:77–95
- Iponga DM, Milton SJ, Richardson DM (2009) Reproductive potential and seedling establishment of the invasive alien tree *Schinus molle* (Anacardiaceae) in South Africa. *Austral Ecol* 34:678–687
- Izhaki I, Safriel UN (1990) The effect of some Mediterranean scrubland frugivores upon germination patterns. *J Ecol* 78:56–65
- Jaksic F (2001) Spatiotemporal variation patterns of plants and animals in San Carlos de Apoquindo, central Chile. *Rev Chil Hist Nat* 74:477–502
- Jiménez HE, Armesto JJ (1992) Importance of the soil seed bank of disturbed sites in Chilean matorral in early secondary succession. *J Veg Sci* 3:579–586
- Jordano P, García C, Godoy JA, García-Castaño JL (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proc Natl Acad Sci USA* 104:3278–3282
- Keeley JE (1995) Seed-germination patterns in fire-prone Mediterranean climate regions. In: Arroyo MTK, Zedler PH, Fox MD (eds) Ecology and biogeography of Mediterranean ecosystems in Chile, California and Australia. Springer-Verlag, New York, USA, pp 239–273
- Kelly D, Ladley JJ, Robertson AW (2004) Is dispersal easier than pollination? Two tests in New Zealand Lorantheae. *New Zealand J Bot* 42:89–103
- Linnebjerg JF, Hansen DF, Olesen JF (2009) Gut passage effect of the introduced red-whiskered bulbul (*Pycnonotus jocosus*) on germination of invasive plant species in Mauritius. *Austral Ecol* 34:272–277
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858
- Nathan R (2006) Long-distance dispersal of plants. *Science* 313:786–788
- Paulsen TR, Högstedt G (2002) Passage through bird guts increases germination rate and seedling growth in *Sorbus aucuparia*. *Funct Ecol* 16:608–616
- Randall RP (2002) A global compendium of weeds. RG and FJ Richardson, Melbourne, Australia
- Reid S (2008) Interaction dynamics of avian frugivores and plants in a subAndean sclerophyllous shrubland of central Chile: implications for seed dispersal and regeneration patterns. PhD Dissertation, Pontificia Universidad Católica de Chile, Santiago, Chile
- Reid S, Armesto JJ (2010) Interaction dynamics of avian frugivores and plants in a Chilean Mediterranean shrubland. *J Arid Environ*
- Robertson AW, Trass A, Ladley JJ, Kelly D (2006) Assessing the benefits of frugivory for seed germination: the importance of the deinhibition effect. *Funct Ecol* 20: 58–66
- Russo SE, Portnoy S, Augspurger CK (2006) Incorporating animal behaviour into seed dispersal models: implications for seed dispersal. *Ecology* 87:3160–3174
- Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Ehuenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774
- Samuels IA, Levey DJ (2005) Effects of gut passage on seed germination: do experiments answer the questions they ask? *Funct Ecol* 19:365–368
- Schupp EW (1993) Quantity, quality and the effectiveness of seed dispersal by animals. In: Fleming TH, Estrada A (eds) Frugivory and seed dispersal: ecological and evolutionary aspects. Kluwer Academic, Dordrecht, The Netherlands, pp 15–29
- Skarpaas O, Dauer JT, Schwarz CM, Rauschert EJ, Jongejans E, Jabbour R, Mortensen DA, Isard SA, Lieb DA, Sezen Z, Hulting AJ, Ferrari MJ, Shea K, Long ES (2007) Dispersal: towards unification across organisms and research traditions. Movement ecology symposium, 92nd annual meeting of the ecological society of America. San Jose, California, 4–10 Aug 2007
- Traveset A (1998) Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspect Plant Ecol Evol Syst* 1:151–190
- Traveset A, Verdú M (2002) A meta-analysis of the effect of gut treatment on seed germination. In: Levey DJ, Silva WR, Galetti M (eds) Seed dispersal and frugivory: ecology, evolution and conservation. CABI Publishing, Wallingford, UK, pp 339–350
- Traveset A, Riera N, Mas RE (2001) Passage through bird guts causes interspecific differences in seed germination characteristics. *Funct Ecol* 15:669–675
- Traveset A, Robertson AW, Rodríguez-Pérez J (2007) A review on the role of endozoochory in seed germination. In: Dennis AJ, Schupp EW, Green RJ, Westcott DW (eds) Seed dispersal: theory and its application in a changing world. CABI Publishing, Wallingford, UK, pp 78–101