



Are birds, wind and gravity legitimate dispersers of fleshy-fruited invasive plants on Robinson Crusoe Island, Chile?



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ABSTRACT

Although fleshy-fruited species are usually dispersed by animals and gravity, previous research shows that the fleshy fruits of invasive plants on Robinson Crusoe Island (RC) are also moved by wind. To determine whether a bird (*Turdus falcklandii*), wind, and gravity could be legitimate dispersers of fleshy fruits from the invasive plant species *Aristotelia chilensis*, *Rubus ulmifolius* and *Ugni molinae*, we carried out germination trials with seeds defecated by *T. falcklandii* and hand-cleaned in the laboratory, and added another trial in field conditions, sowing intact fruits. Whole fruits sown intact are used to represent dispersal by wind or gravity. The field trials for *A. chilensis* and *R. ulmifolius* were performed in canopy gaps and closed forests to evaluate the effect of shadow on seedling emergence. Field trials for *U. molinae* were only established in open shrubland, since this species does not occur in forests on RC. Laboratory trials showed gut-passed *A. chilensis* seeds increased the germination percentage while gut-passed seeds did not affect germination in *R. ulmifolius* and *U. molinae*. In the field, trials revealed that seeds from intact fruits germinated in a similar way to gut-passed or hand-cleaned seeds, with the exception of *U. molinae*, which did not germinate inside fruits. In all field treatments, the germination percentage of *A. chilensis* and *R. ulmifolius* was higher in the canopy gaps than under closed canopy. These results indicate that *T. falcklandii* is a legitimate disperser for the three invasive species studied on RC. Wind and gravity should also be considered legitimate dispersers of *A. chilensis* and *R. ulmifolius*. Microhabitat (i.e., canopy gaps) plays a more important role in improving the establishment of *A. chilensis* and *R. ulmifolius* than the dispersal mechanism itself.

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1. Introduction

Seed dispersal of fleshy-fruited invasive plants by vertebrates, specifically birds, is a common cause of naturalization and expansion of exotic plants that may influence the subsequent alteration of environments (Gosper et al., 2005). This phenomenon has been described on many oceanic islands (Chimera and Drake, 2010; Smith-Ramírez et al., 2013; Williams, 2006). When ingested, the vertebrate's gut produces seed coat scarification, which in some cases enhances and/or accelerates germination (Traveset, 1998; Traveset et al., 2001). Additionally, vertebrates remove the peri-

carp, eliminating inhibitors present in the pulp that impede or delay seed germination (Samuels and Levey, 2005).

Even though endozoochory (i.e., ingestion by vertebrates) is by far the most extensively studied dispersal mechanism for fleshy fruits, barochory (gravity-dispersed) and anemochory (wind-dispersed) are other frequent vectors to disperse fruits (Armesto et al., 2001; Guan et al., 2006; McAlpine and Jesson, 2008; Smith-Ramírez et al., 2013). When seeds of fleshy fruits are dispersed by wind or gravity they remain inside the pericarp. Seeds of some species can germinate inside the fruit, or remain viable inside the fruit until environmental conditions or other agents break the husk and pulp, but others can die if that does not happen (Figueroa and Castro, 2002; Robertson et al., 2006; Yagi-hashi et al., 1998, 1999, 2000). Samuels and Levey (2005) conducted a literature review of 99 articles and found only 22 studies in which germination was studied in intact fruits, a common seed fate in natural conditions. Lack of these types of germination studies, par-

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ticularly in the field, is an issue. Studies focusing solely on dispersal by vertebrates fail to take into account the role of the pulp when it is not removed by dispersal agents (i.e. in wind and gravity dispersal). Despite its potential importance to the field of ecology and restoration, there is a clear disparity between published literature relating to dispersal effectiveness of animals when compared to the obvious dearth in studies of dispersal by wind or gravity (see review in Schupp et al., 2010). Evidence supporting the role of vertebrates in dispersal and establishment is clear and should not be discounted. However, if ripe fruits are light and the wind is strong anemochory and barochory are not unusual seed dispersal vectors, and have even been found to complement dispersal by birds on Taiwan (Guan et al., 2006) and on Robinson Crusoe Island (Smith-Ramírez et al., 2013).

Robinson Crusoe Island (RC) is part of the Juan Fernandez Archipelago (JFA) in the South Pacific off the Chilean coast. The JFA is a Chilean Biosphere Reserve and one of the world's most threatened biotas (Wester, 1991). RC has been considered the island with the highest endemism per m² in the world (Stuessy, 1992). Flora in the JFA is going to face a marked reduction in the short term due to the expansion of introduced plant species (Dirnböck et al., 2003; Smith-Ramírez et al., 2013). The most invasive plants on RC are three fleshy-fruited shrub species: *Aristolotelia chilensis* (Molina) Stuntz (Elaeocarpaceae), *Rubus ulmifolius* Schot (Rosaceae) and *Ugni molinae* Turcz. (Myrtaceae). In forests, *A. chilensis*, *R. ulmifolius*, and *U. molinae* seeds are thought to be dispersed mainly by *Turdus falcklandii* Quoy & Gaimard (Turdinae), a bird widely distributed in all habitat types on RC (Hahn et al., 2011). However, it is uncertain whether *T. falcklandii* is actually a legitimate disperser of these species. In the case of *A. chilensis* seeds, *T. falcklandii* was found to move 82.1% of the seeds out of its parental tree while 17.9% was moved by wind (Smith-Ramírez et al., 2013). Moreover, *R. ulmifolius* and *U. molinae* are dispersed by wind, but less frequently than for *A. chilensis* seeds (Smith-Ramírez et al., 2013). On the other hand, germination and seedling emergence of *A. chilensis* and *R. ulmifolius* (and probably *U. molinae*) might be affected not only by dispersal vectors, but also by the forest canopy because these are light-demanding species (Arellano-Cataldo and Smith-Ramírez, 2016).

The goal of this study was to investigate the effects of seed dispersal vectors on seed germination of the invasive fleshy fruit plants *A. chilensis*, *R. ulmifolius* and *U. molinae* dispersed by *T. falcklandii*, wind and gravity in laboratory and field condition experiments. We ask 1) Are the above mentioned vectors legitimate seed dispersers? 2) What are their effects on seed germination percentage? 3) Are pulp removal and microhabitat (gap vs. non-gaps) important for seedling emergence in field conditions? To determine whether wind and gravity are legitimate seed dispersers, we sowed intact fruits (with pulp) in the field and evaluated seedling emergence. Here, sowing intact fruits was used as a proxy for wind and gravity. The pulp presence has been considered amply in scientific literature as an adequate indicator of seed dispersal by wind and gravity (Armesto et al., 2001; Guan et al., 2006; Iida and Nakashizuka, 1998; McAlpine and Jesson, 2008).

2. Methods

2.1. Seed collection

The seed collection took place in the middle of the fructification season of each species on RC. That was February for *A. chilensis* and *R. ulmifolius* (austral summer), and early May for *U. molinae* (austral autumn). In 2010 we collected 209 fresh *T. falcklandii* feces and around 200 fruits from *R. ulmifolius* and *A. chilensis* scrubs about 10 m apart each other. The collection of feces and fruits were made

on the forest trails El Mirador de Selkirk and Plazoleta El Yunque on RC. In the field, the seeds were extracted from feces or fruits. Some of the seeds were kept at 5 °C (ca. 3 weeks) before being moved to the laboratory on the mainland and the others were used in field experiments. In May 2011 we collected 102 fresh *T. falcklandii* feces and 200 *U. molinae* fruits from Plazoleta El Yunque. *Ugni molinae* seeds were stored and transported inside feces or intact fruits to be extracted in the laboratory in order to protect their recalcitrant seeds from desiccation (Figueroa et al., 2004).

2.2. Laboratory experiments

To evaluate the effect of seed ingestion by *T. falcklandii* on the germination of *A. chilensis*, *R. ulmifolius* and *U. molinae*, a laboratory trial was conducted comparing defecated and non-defecated hand-extracted seeds. We did not perform trials with intact fruits in the laboratory. It is common to find null germination in laboratory assays because differences between the laboratory and natural environment (Robertson et al., 2006). Two hundred forty defecated and hand-cleaned seeds collected from RC were washed in a 2% chlorine solution to remove pulp residues and to prevent fungal contamination. Thereafter, 30 seeds for each treatment were laid on paper in four petri plaques, with a total of 120 defecated and hand-cleaned seeds per treatment. The seeds were placed inside a germination chamber at 20 °C with a light/darkness photoperiod of 12 h. One or two times per week the plaques were moistened until the paper was saturated.

After 372 days, little germination (no more than 10%) was obtained in *R. ulmifolius* and *A. chilensis*. This is a low germination percentage especially in comparison with similar studies published by Traveset et al. (2001) for *R. ulmifolius* and by Figueroa (2003) for *A. chilensis*. Then, we decided to expose *R. ulmifolius* and *A. chilensis* seeds to cold stratification (5 °C, for 35 days) inside plastic bags. These treatments improve germination of various *Rubus* spp. (Ellis et al., 1985) and we proceeded in a similar way with *A. chilensis*, although stratification is not imperative to improve germination levels of this species (Figueroa, 2003). Afterwards, the bags were kept at room temperature in the laboratory (mean 20 °C) without light for 60 more days. *Ugni molinae* seeds successfully germinated and did not need stratification. Germination (i.e. radicle emergence) was registered every 1–3 days during the first 4 months, and thereafter every week for 9 months. The recording time amounted to 467 days for both *A. chilensis* and *R. ulmifolius* and 322 days for *U. molinae*. Upon the final recording, tetrazolium tests and visual examination of seeds and embryos were performed.

2.3. Field experiments

To evaluate seed dispersal effects by *T. falcklandii* (seeds without pulp), wind, and gravity (seeds with pulp) in the field we conducted germination trials with defecated, non-defecated seeds and in addition intact fruits. The dormancy of seeds from intact fruits collected from the plants may be lower and the seed viability could be higher than fruits that remain on the ground or underground for weeks or months. Although there may be some differences between seeds collected on the plant vs. on soil, we decided to use seeds collected from plants in the assays (to represent wind and gravity dispersal). We then compared their germination with seeds collected in fresh feces, recognizable by the presence of fecal residue that had not been washed away by rain. Both groups of fresh seeds were sown at the same time, which had the advantage of producing comparative data.

Aristolotelia chilensis and *R. ulmifolius* trials were carried out in February 2010 in the Plazoleta El Yunque (PEY) forest stand. The trials were made in canopy gaps and closed forest. We chose four forest canopy gaps in PEY (gap sizes = 110–360 m²), and four closed

forest sites. For each site, 30 seeds or fruits (one drupe in the case of *R. ulmifolius*) from each species per treatment (gut-passed, hand-cleaned and fruits) were sown in a plot of 600 cm² (20 cm × 30 cm). After the leaf litter was removed from the plots, seeds and fruits were distributed evenly and sown one cm deep. Metallic nets covered with fine polyester were used to protect the plots from herbivores and rain. Seedling emergence was recorded once a month for one year. On average, each *A. chilensis* fruit has two seeds: very rarely, one or three seeds can be found. We planted one drupe of *R. ulmifolius* containing one seed.

One km north of PEY we selected a scrubland site (without canopy cover) to sow *U. molinae* seeds. The seeds were sown two meters from where adult *U. molinae* plants were naturally growing; this species grows only in large open areas, not in the forest. The gut-passed, hand-cleaned seeds and intact fruits were sown in four plots, each of them containing 30 seeds or fruits. On average, each *U. molinae* fruit from the study area had 11.3 seeds ($n = 20$ fruits). The trial took place in June 2012 and seed germination was recorded following the same protocol mentioned for *A. chilensis* and *R. ulmifolius*. *Ugni molinae* seeds were not planted under canopy or in small or medium canopy gaps since this species never grows in these places on RC (Díaz, 2013).

2.4. Data analysis

We used the cumulative germination percentages of each replica at the end of the experimental period, both in the laboratory (467 days) and in the field (12 months), to analyze the data. Analyses of variance (ANOVA) were conducted comparing the germination of defecated and hand-cleaned seeds for each species in the laboratory. The field germination was analyzed using two factors ANOVA for *A. chilensis* and *R. ulmifolius*, evaluating microhabitat effect, seed treatments, and their interactions. To evaluate *U. molinae* seed treatment in the field we used a Kruskal-Wallis test.

3. Results

3.1. Germination in the laboratory

The three invasive species were able to germinate after passing through the gut of *T. falcklandii*, but the response varied among species. Chamber germination of *A. chilensis* gut-passed seeds began 26 days after starting the trial, with a final germination percentage (372 days after sowing) that reached 19.2%, whereas non gut-passed seeds reached 1.0%. After the stratification period, the final accumulated germination in *A. chilensis* was significantly higher for gut-passed than for hand-cleaned seeds, with 22.5% and 5.0%, respectively ($F_{(1,6)} = 12.850$, $P = 0.0116$; Fig. 1).

Rubus ulmifolius gut-passed seeds started germination after 180 days while hand-cleaned seeds started germination 117 days after sowing, reaching percentages of 3.3% and 6.7%, respectively. After the stratification period, the final accumulated germination percentage was 42.5% for gut-passed and 50.8% for hand-cleaned seeds, but these differences were not significant ($F_{(1,6)} = 2.381$, $P = 0.1740$; Fig. 1).

Ugni molinae gut-passed seeds started germination after 15 days and hand-cleaned seeds 21 days after sowing. In both germination treatments, *U. molinae* seeds showed germination during the first three months, particularly in hand-cleaned seeds. Final germination percentages were slightly higher for hand-cleaned seeds, but not significantly different from defecated seeds (96.0 vs 87.4%, respectively) ($F_{(1,6)} = 3.845$, $P = 0.0976$; Fig. 1). Tetrazolium test suggested the remaining seeds were incapable of germination.

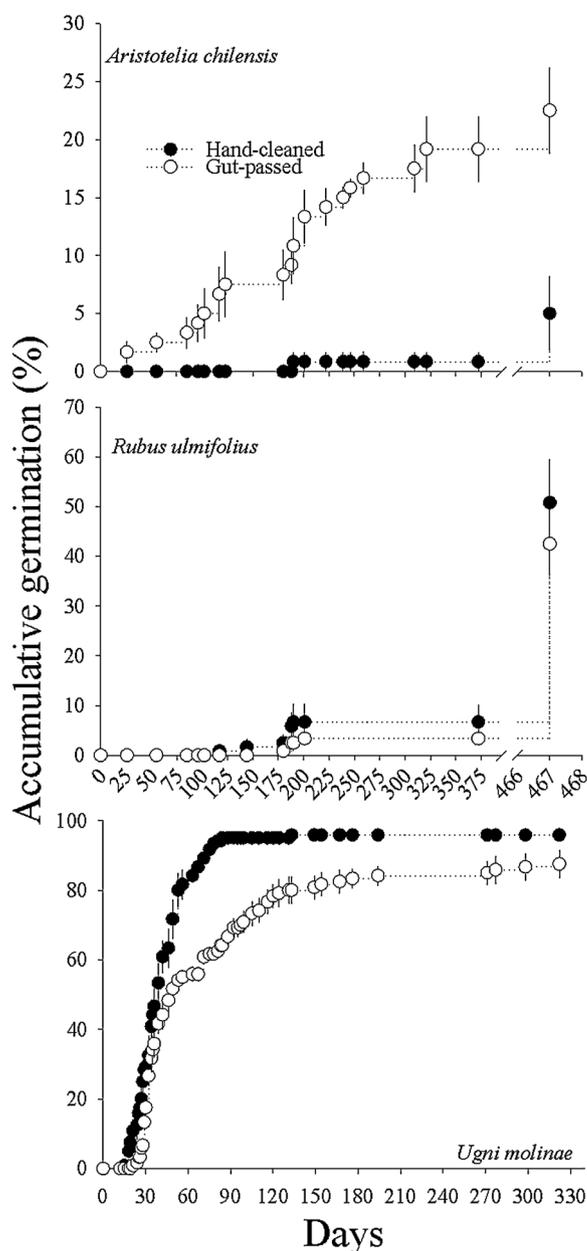


Fig. 1. Accumulative germination curves of seeds defecated by the bird *Turdus falcklandii* (gut-passed) and not defecated (hand-cleaned seeds through a manual extraction of the pulp) belonging to three invasive species (*Aristotelia chilensis*, *Rubus ulmifolius* and *Ugni molinae*) on Robinson Crusoe Island, Chile. Circles are mean (\pm SE) germination time ($n = 4$ petri dishes with 20 seeds each). Seeds were germinated in a germination chamber. On day 467, the final percentage after cold stratification of *A. chilensis* and *R. ulmifolius* is shown (see methods). *Ugni molinae* seeds did not need stratification.

3.2. Seedling emergence in the field

The seeds of *A. chilensis* and *R. ulmifolius* began to germinate in September (ca. 7 months after sowing). The seedling emergence of both *A. chilensis* and *R. ulmifolius* took place in all seed treatments (gut-passed, hand-cleaned, and intact fruits) in a relatively similar way, although it was greater in intact fruits in relation to other treatments. The highest percentage of emergence occurred in canopy gaps (ca. 10%) and the lowest in closed forest (ca. 1%), irrespective of the seed treatments (Fig. 2). The highest emergence rates were seen in intact fruits sown in forest canopy gaps, with 18.0% in *A. chilensis* and 12.0% in the case of *R. ulmifolius* (Fig. 2).

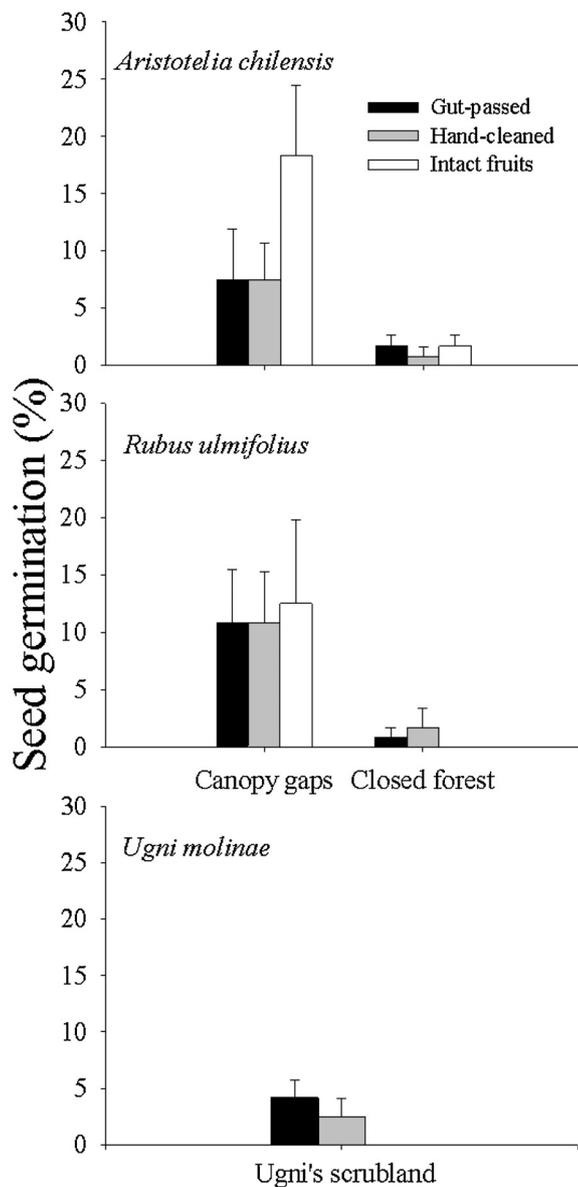


Fig. 2. Seedling emergence (mean \pm SE) under field conditions of three invasive species on Robinson Crusoe Island. Seeds came from *Turdus falcklandii* feces (gut-passed), pulp manually hand-cleaned and intact fruits. Seeds of *Aristotelia chilensis* and *Rubus ulmifolius* were sown in canopy gaps and closed forests. Seeds of *Ugni molinae* were sown in open areas (Ugni's scrubland).

We did not find interaction between the presence of canopy forests and treatments for either invasive species (*A. chilensis*: $F_{(2,18)} = 0.524$, $P = 0.6011$; *R. ulmifolius*: $F_{(2,18)} = 0.077$, $P = 0.9258$). Differences in seedling emergence from gut-passed, hand-cleaned, and intact fruits were not significant for *A. chilensis* ($F_{(2,18)} = 0.748$, $P = 0.4987$) and *R. ulmifolius* ($F_{(2,18)} = 0.139$, $P = 0.8714$). For both species, only the presence or absence of canopy forest significantly affected seedling emergence, with a higher percentage in forest canopy gaps than under closed forests (*A. chilensis*: $F_{(1,18)} = 11.364$, $P = 0.0034$; *R. ulmifolius*: $F_{(1,18)} = 16.521$, $P = 0.0007$).

Seedling emergence of *U. molinae* took place from November to January (austral spring and summer). In general, the rate was low: 4.1% for defecated seeds and 2.5% for hand-cleaned seeds. Seeds from intact fruits did not germinate and decomposed within a month. The difference between treatments was not significant (Kruskal-Wallis test, $\chi^2 = 5.05$, $df = 2$, $P = 0.08$).

4. Discussion

Our results show that *T. falcklandii* is a legitimate seed disperser (it defecates viable seeds) of the three most important invasive woody species on RC. In the laboratory the seed germination response of each plant was species-specific. The germination of *A. chilensis* seeds increased when they had been gut-passed by *T. falcklandii* (17% more than when hand-cleaned). *Rubus ulmifolius* seeds were not affected by gut-passing. In the case of *U. molinae*, gut-passed seeds showed a non-significant decrease in germination (12% less than for hand-cleaned seeds). These results suggest a positive chemical or mechanical abrasive effect on the seed coat during ingestion by *T. falcklandii* only in the case of *A. chilensis*. The results of our study coincide with the findings in other experiments carried out across Europe with *R. ulmifolius* seeds passed through the gut of *Turdus* (Clergeau, 1992; Rodríguez-Perez et al., 2005; Traveset et al., 2001), on mainland Chile with *A. chilensis* seeds dispersed by birds (including *T. falcklandii*) (Valdivia and Simonetti, 2007), and *U. molinae* seeds ingested by a marsupial (*Dromiciops gliroides*) (Mora and Soto-Gamboa, 2011). Unlike the hand-cleaned and gut-passed germination in the laboratory, in the field *A. chilensis*, *R. ulmifolius* and *U. molinae* seedling emergence was not affected by seed treatments (gut-passed, hand-cleaned, and intact fruits). Different responses of seed germination in the laboratory and field have been reported and these differences must be caused by environmental factors (physical and/or biological) that prevent germination *in situ*; these factors can be the presence of fungi, chemicals, or soil characteristics (Rodríguez-Perez et al., 2005).

In the field experiments, non-significant differences in seedling emergence were caused by seed treatments. Thus, neither the chemical, mechanical nor disinhibition effect are important for the invasive process of these three species on RC. *Turdus falcklandii* plays a more important role, transporting seeds all over the island. For all three species, it is particularly important that seeds land in microsites that aid germination, such as forest canopy gaps (*A. chilensis* and *R. ulmifolius*) or big open areas (*U. molinae*). Indeed, seed dispersal to "safe sites" is one of the most important functions of birds as dispersers (Deckers et al., 2008; Schupp, 1995), including invasive species on oceanic island ecosystems (McAlpine and Jesson, 2008). Smith-Ramírez et al. (2013) showed that *T. falcklandii* is responsible for moving *A. chilensis* and *R. ulmifolius* seeds to forest canopy gaps, especially to the gap borders where they can germinate. Probably, the same behavior as described for *T. falcklandii* on the mainland, consuming a high quantity of fruits on perch and looking for food on the soil (Amico and Aizen, 2005), contributes to highly invasive seedlings on RC (Arellano-Cataldo and Smith-Ramírez, 2016).

Considering that the pulp does not inhibit the germination of *A. chilensis* and *R. ulmifolius* in field conditions, and wind and gravity move the fruits, we propose that these agents, in addition to *T. falcklandii*, are legitimate seed dispersers. In contrast, *U. molinae* seed germination is inhibited by pulp, and only *T. falcklandii* is a legitimate disperser for this invasive species on RC. The low germinability of hand-cleaned and gut-passed *U. molinae* seeds in the field compared with the same treatment in the laboratory suggests that these seeds are probably affected by fungi and/or desiccation, because their seeds have a thin cover and little endosperm (Figueroa et al., 2004; Ramírez et al., 1980). We found that *U. molinae* fruits, and the seeds inside it, rotted quickly in natural conditions, as was observed in field trials with other Myrtaceae seeds from southern Chile (*Luma apiculata* and *Myrceugenia planipes*) (Figueroa and Castro, 2002).

The maximum wind speed on RC is in January and February (Hajek and Espinoza, 1987) when *A. chilensis* and *R. ulmifolius* are at the fruiting peak. The average speed of the wind is 8 km/h, with a maximum of 78 km/h (Hajek and Espinoza, 1987). It has been

widely accepted that the wind moves seeds shorter distances than birds (Howe and Smallwood, 1982), but wind dispersal could be complementary to bird and gravity dispersal in moving seeds of light fleshy fruits, especially in areas where there are strong winds, as is the case on RC or other islands, as Taiwan by sassafras fruits (Guan et al., 2006). Since each *R. ulmifolius* polidrupe has an average of 23 seeds, the occurrence of an infrequent dispersal event may move a large number of seeds at the same time, from exotic scrubland or invaded forest gaps to inside forest or other gap forests.

For *A. chilensis* and *R. ulmifolius*, in all seed treatments (hand-cleaned, gut-passed, and intact fruits) germination was better in canopy gaps than under closed forest. The low germination rate under closed forest does not diminish the importance of *T. falcklandii* and wind on the invasion of *A. chilensis* and *R. ulmifolius*. Germination under forests explains the seedling banks of *A. chilensis* and *R. ulmifolius* found in RC forests by Arellano-Cataldo and Smith-Ramírez (2016). On the other hand, gravity made a substantial contribution to seed dispersal of these invasive species on RC, accounting for around 97.6% of seeds dispersed (Smith-Ramírez et al., unpublished data), but down the parental invasive scrubland we never saw any kind of seedlings. The soil seed bank lasted one or two years in the case of *R. ulmifolius*, and there are no seed banks in the case of *A. chilensis* (Smith-Ramírez et al., 2013).

We conclude that *T. falcklandii*, wind and gravity are legitimate seed dispersers of the two invasive species, *A. chilensis* and *R. ulmifolius*. *Turdus falcklandii* is a legitimate disperser of *U. molinae*, but wind or barochory probably is not, unless the fruits dispersed are quickly broken and probable seed germination inhibitors are removed. The effects of seeds passing through the gut of *T. falcklandii* are not relevant in relation to moving them to adequate places. Finally, we propose that in some cases wind can cause effective dispersal of fleshy fruits, such as *A. chilensis* and *R. ulmifolius*.

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