Are pulp consumers effective seed dispersers? Tests with a large-seeded tropical relict tree

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ABSTRACT

Several plant species in the Neotropics bear large, fleshy fruits that suggest adaptation to endozoochorous seed dispersal by large vertebrates. Many of these plants occur in areas where large vertebrates are no longer present; consequently, their seeds are dispersed by pulp consumers; small vertebrates that only ingest the pulp reward because they are uncapable of swallowing the fruits whole. Few studies have examined the role of these pulp consumers on the regeneration of large-fruited/seeded plants. Here, we assessed seed disperser effectiveness (SDE) and context-dependence in SDE of pulp consumers of *Pouteria splendens*, a large-seeded tree, considered a tropical relict in Mediterranean Chile. We found that *P. splendens* fruits are consumed by six species of non-flying vertebrates; four of which act as dispersers with very low effectiveness. Low SDE resulted from the quantitative, rather than the qualitative component, specifically from low visitation rates. Most seeds remained under *P. splendens* trees, either from being dispersed there or because they were not dispersed at all. However, both emergence and establishment probabilities were higher under conspecific plants than in other habitats, suggesting no negative density-dependent effects on *P. splendens* recruitment. Although the absence of more effective dispersers does not seem to affect local recruitment probabilities, it results in the absence of long-distance dispersal, further isolating the remnant *P. splendens* populations. Finally, although pulp consumers have very low disperser effectiveness, the key functional role of these species is to remove the fleshy pulp from *P. splendens*' seed as its presence significantly reduces germination probability.

Abstract in Spanish is available with online material.

SEED DISPERSAL BY VERTEBRATES IS WIDELY ACKNOWLEDGED AS A KEY PROCESS FOR THE PERSISTENCE OF MANY PLANT POPULATIONS because by removing fruits and dispersing seeds, animals enable plants to colonize new habitats, reach suitable sites for establishment, and escape from density-dependent mortality close to the parents (Janzen 1970, Connell 1971, Howe & Smallwood 1982, Howe & Miriti 2004). Therefore, absence of dispersers or a decrease in their availability is expected to reduce population growth (Nathan & Muller-Landau 2000, Dalling *et al.* 2002), disrupt gene flow among populations (Bacles *et al.* 2006), and ultimately increase the probability of extinction of the plant species that depend on them (Cordeiro & Howe 2003, Levin *et al.* 2003, Galetti *et al.* 2006, Traveset *et al.* 2012). Fruit removal *per se*, however, does not guarantee plant recruitment because not all dispersed seeds are able to establish (Wang & Smith 2002). In this light, disperser behavior is expected to affect the quality of the seed dispersal services provided.

A frugivores' seed dispersal effectiveness (SDE) is a function of the number of seeds it disperses (*i.e.*, the quantitative component) and the probability that these seeds establish (qualitative component) (Schupp 1993, Schupp *et al.* 2010). Some dispersers are very effective because they remove large quantities of seeds and/or disperse them in habitats that are suitable for recruitment; others are less effective or not effective at all, because they disperse few seeds per visit or because these seeds fail to establish (Calviño-Cancela & Martin-Herrero 2009, Fedriani & Delibes 2009, Loayza & Rios 2014). SDE depends partially on the mode frugivores handle and process seeds. In general, vertebrates that swallow the fruit whole and defecate or regurgitate intact seeds (*i.e.*, that provide endozoochorous dispersal) are considered more effective dispersers than vertebrates which, unable to swallow fruits whole, only ingest the fruit reward without dispersing the seeds (*i.e.*, pulp consumers) (Jordano & Schupp 2000). Indeed, the latter are often considered as cheaters of seed dispersal mutualisms (Olesen *et al.* 2010, Tewksbury *et al.* 2008); nonetheless, in some systems pulp consumers can be effective dispersers by providing sporadic dispersal or because pulp removal *per se* can have positive effects on seed and seedling fate (Fedriani *et al.* 2012, Loayza & Rios 2014). Finally, although species differ in their mean SDE, this parameter can vary with the biotic and abiotic context (Perea *et al.* 2013, Pesendorfer *et al.* 2016). Therefore, in environments with temporally variable conditions, a frugivores' SDE may vary across years.

In the Neotropics, there are several plant species with fruits and seeds that are too large to be swallowed and endozoochorically dispersed by the extant wildlife. Some of these species have presumably lost their endozoochorous dispersers at the end of the Pleistocene when many large Neotropical herbivores went extinct (Janzen & Martin 1982), while others have lost their dispersers more recently, as a result of 'Anthropocene defaunation' (Dirzo *et al.* 2014). In either case, essential seed dispersal services to these large-fruited/seeded plants are now carried out exclusively by pulp consumers (*e.g.*, de Almeida & Galetti 2007, Hirsch *et al.* 2012, Loayza *et al.* 2014, Luna *et al.* 2016), but whether the seed dispersal they provide is effective or not seems to be species-specific. For example, agoutis provide effective dispersal to *Astrocaryum standleyanum,* a large-seeded palm with a megafaunal dispersal syndrome (Hirsch *et al.* 2012, Jansen *et al.* 2012). In contrast, the small vertebrates that persist in disturbed forests of Uganda are presumably not effective dispersers of the large-fruited/seeded plants that remain in these forests. For most large-fruited/seeded plant species that have lost their endozoochorous dispersers, however, little is known on whether the seed dispersal services provided by vertebrates uncapable of ingesting seeds are effective or not.

Pouteria splendens is a narrow endemic tree of central Chile with little natural recruitment. This species produces large-seeded, fleshy fruits that fit the Type I megafaunal fruit syndrome described by Guimaraes *et al.* (2008). The fauna that co-occurs with *P. splendens* are mainly small pulp consumers and seed predators; there are no frugivorous mammals along its distribution, or birds with a gape wide enough to swallow its fruits (Armesto *et al.* 1987, Sotes *et al.* 2013). Given this scenario, we hypothesized that dispersers of *P. splendens* fruits do not provide effective dispersal services to this plant. Specifically, we expected (1) that dispersers would remove few fruits per visit in account of the fruits' large size and the inability of vertebrates to swallow the fruit whole, (2) vertebrates to disperse most seeds close to parent plants, and (3) low recruitment probabilities in this habitat due to negative density-dependent processes. Additionally, because of inter-annual variability associated with semiarid environments of Central Chile, we expected context-dependence in the SDE of different dispersers. To test these predictions, we examined the quantitative and qualitative components of SDE by video-monitoring rates of fruit removal by each frugivore, determining habitats of seed deposition, and experimentally quantifying emergence and seedling survival probabilities in the seed deposition habitats during two fruiting seasons.

METHODS

STUDY SITE AND SPECIES.—We conducted this study from 2015 to 2017 in Bioparque Puquén and its surroundings. Bioparque Puquén is a private park located in Los Molles, Chile (32°15′ S, 71°30′ O); this area corresponds to a transitional zone between sclerophyllous shrublands and woodlands (Lund & Teillier 2012) and contains the largest and most continuous population of *P. splendens*. The study site has a semiarid Mediterranean climate, with long and dry summers and wet and cold winters (Di Castri & Hajek 1976). Mean annual precipitation is approximately 312 mm and is characterized by a marked seasonality, with 70 percent of the rain falling during the winter and <2 percent during the summer (Lund & Teillier 2012). Mean annual temperature is 14.4°C, with thermal amplitude of 5°C between the mean temperatures in January and July. The dominant plant species in the study area are *Pouteria splendens, Lithrea caustica, Fuchsia lycioides,* Bahia *ambrosioides, Baccharis macraei, Sphacele salvia,* and *Eupatorium salvia* close to the coast, and *P. splendens* and *Peumus boldus* inland.

Pouteria splendens (A.DC) Kuntze (Sapotaceae) is an evergreen woody plant, endemic to Central Chile. It is the only representative of the Sapotaceae in Chile and is considered a tropical relict in a semiarid Mediterranean ecosystem (Gajardo 1994, Francois 2004). This species grows as small trees (<5 m) inland and as shrubs when it is close to the coast (Sotes *et al.* 2013, Morales *et al.* 2015). It has an intricate branching physiognomy, and adult plants generally grow at high densities in discrete patches (pers. obs.). Seedlings are uncommon and found almost exclusively under conspecific plants (Sotes *et al.* 2013). *P. splendens* has sclerophyllous leafs, which accumulate under the canopy forming a thick leaf litter layer that is considered key both for seed and seedling survival (Sotes *et al.* 2013, 2018). Flowering and fruiting occur simultaneously between September and April; however, the peak of the fruiting season is between December and February (Henríquez *et al.* 2012). Fruits are red or yellow fleshy drupes with a sweet, edible pulp. They measure on average 2.6 cm × 2.7 cm (width and length) but can be as large as 3 cm × 4 cm; they weigh between 2.65 and 15.6 g (8.5 g ± 2.1, mean ± s.d.). Each fruit typically encloses a single recalcitrant seed measuring up to 22 mm × 30 mm (mean: 18 mm × 22 mm) (CV = 13%, $N = 160$) and weighing 4.08 g ± 2.1 (Peña-Egaña 2017). When ripe, fruits fall to the floor where ground-dwelling vertebrates can remove them. There is no published information on *P. splendens'* seed dispersal and only one reference of birds pecking on the fruits' fleshy pulp (*Turdus falklandii* and *Diuca diuca*; Armesto *et al.* 1987). Moreover, there are no predominantly frugivorous vertebrates present along its distribution, only herbivores, insectivores, and carnivores that occasionally include fruits in their diet. Among these species—and in addition to *T. falklandii* and *D. diuca*—are two birds (*Columba araucana* and *Sturnella loyca*) and eight mammals (*Pseudalopex griseus*, *P. culpaeus* and *Conepatus chinga*, *Abrothrix longipilis*, *A. olivaceus*, Octodon *degus*, *O. lunatus*, and *Phyllotis darwini*). Of these, only foxes (*Pseudalopex* spp.) and the skunk (*C. chinga*) are large enough to potentially swallow whole fruits. Currently, *P. splendens* remains only in nine sites within its original distribution (Morales *et al.* 2015) and is considered as critically endangered by Squeo *et al.* (2001) and Hechenleitner *et al.* (2005).

QUANTITATIVE COMPONENT OF SEED DISPERSAL.—To identify the vertebrates that consume *P. splendens* fruits and determine the number of fruits removed per visit, we established 42 experimental stations consisting of 15 fruits each, which came from a pool of fruits collected in the study area from multiple trees (>30). Individual stations were placed underneath fruiting *P. splendens* trees that were separated by at least 30 m and located far from

trails. Within each station, all fruits were individually marked with a 15-cm-long (0.25 mm thick) plastic thread, which passed through the seed and had a small piece of flagging tape (with experimental station and fruit number) attached to one end. Fruit removal in each station was monitored using video recordings. In 2015, we monitored 31 trees with GoPro Hero 3 cameras for five consecutive days during January and February, from 0700 h thru 2100 h. In January 2016, we monitored 11 trees for 12 consecutive days and nights using Reconyx ScoutGuard SG560C and Bushnell Trophy Cam Aggressor Low Glow cameras. Cameras were placed between 50 and 100 cm from the ground and 1–2 m from the experimental station; the field of view ranged from approximately 4–10 m. In both years, we recorded (1) the identity of the species removing fruits, (2) the number of visits per species, (3) the number of fruits removed (*i.e.*, seeds dispersed) per species per visit, (4) the number of fruits with only *in situ* pulp consumption, and (5) the habitat where the fruit was dispersed by a given disperser. We considered a seed as 'dispersed' when it was removed at least 3 m from the experimental station and was no longer beneath the crown radius of the focal tree. Moreover, for the purposes of our study, a dispersed 'seed' could be the whole fruit, a fruit with the pulp partially consumed and consequently the seed partly exposed, or the cleaned seed with no pulp attached to it.

QUALITATIVE COMPONENT OF SEED DISPERSAL.—*Dispersal habitats.*—We determined the habitats where seeds were dispersed by searching for marked fruits/seeds on the days following the recordings. When a fruit was found, we registered (1) the distance to the focal tree, (2) the habitat where it was found, and (3) the condition of the fruit; that is, if it was intact or if the pulp had been completely or partially consumed.

Habitat suitability for recruitment.—We examined if the habitats where seeds arrived were suitable for seedling recruitment by experimentally quantifying seedling emergence and survival in these habitats. At the end of February in both 2015 and 2016, we established 10 emergence stations in each of the habitats where we recorded seed arrival during the first year, which were (1) open interspaces, (2) under conspecific plants, and (3) dry riverbeds (see Results). Stations ($N = 30$) were separated from each other by at least 30 m, and each station consisted of 20 seeds (with the pulp manually removed), which were partially buried and protected by a wire mesh ($30 \times 20 \times 10$ cm, 8 mm mesh size) to prevent seed removal by vertebrates. Seedling emergence was monitored every 2 mo for 8 mo for both cohorts. At the end of this period, we removed the wire cage, individually marked all seedlings emerged, and monitored their fate 12 and 20 mo after emergence for the 2015 cohort, and for 8 mo after emergence for the 2016 cohort. Finally, we calculated the mean probability of establishment in each habitat (*i.e.*, the probability of seeds to successfully emerge and establish as seedlings in the habitat) by multiplying the probabilities of seedling emergence and seedling survival for each cohort independently.

Seed dispersal effectiveness.—We calculated SDE of the vertebrates that consume *P. splendens* fruits as the product of the quantity (QC) and quality (QL) components of their dispersal services (SDE = QC × QL). The QC was the number of seeds dispersed by each frugivore per 10-h period. The QL was calculated as:

$$QL = \sum_{i=1}^{3} (p_e * p_s * P_d)$$

where p_e is the probability of emergence, p_s is probability of seedling survival and P_d is the proportion of seeds dispersed to a given microhabitat ($N = 3$) (Godínez-Alvarez & Jordano 2007). We calculated mean SDE for each frugivore species for the 2 yr of this study, as well as their SDE for 2015 and 2016 separately to assess variation between years.

Statistical analyses.—We evaluated whether the sampling effort was adequate to capture the assemblage of non-flying vertebrates consuming *P. splendens* fruits using a species accumulation curve generated with EstimateS 9.1.0 (Colwell 2006). We examined whether the total number of dispersed seeds differed among dispersers and between years using a GLM with Poisson error distributions (link = 'log'). We used permutation-based chi-square tests to evaluate (for 2015 and 2016 separately) whether the total number of seeds dispersed by each vertebrate depended on the number of visits to the experimental 'station (*i.e.*, a fruiting tree). The latter were based on 10,000 permutations of the data. We used the same analysis to test whether the frequency of seeds dispersed to each habitat varies between years for each disperser independently and to examine whether the probability of seedling recruitment differed among habitats. Differences in seedling emergence and survival between years and among habitats were assessed using GLMs with Poisson error distributions (link = 'log'). All statistical analyses were performed using the R statistical environment (R Development Core Team 2017).

RESULTS

QUANTITATIVE COMPONENT OF SEED DISPERSAL.—Six species of non-flying vertebrates were recorded consuming *P. splendens* fruits during 2638 h of video monitoring (473 and 2165 h in 2015 and 2016, respectively) (Table 1). The species accumulation curve plateaued after approximately 400 h of video recordings (Fig. S1), which suggests that this is an accurate estimate of the number of (non-flying) vertebrates that consume *P. splendens* fruits in the area. As expected, none of these species provided endozoochorous seed dispersal to *P. splendens*. *Pseudolopex griseus* (South American gray fox)*, Abrothrix olivaceus* (Olive grass mousse) and *Phyllotis darwini* (Darwin's leaf-eared mouse) acted as pulp consumer–dispersers (PCSD; Jordano & Schupp 2000); these vertebrates generally moved fruits a few meters away from the experimental stations and then consumed the pulp leaving the seed intact at the site of consumption. *Conepatus chinga* (Molina's hog-nosed skunk) and *Callipepla californica* (California quail) consumed the pulp but never

TABLE 1. *Dispersal habitats and proportion of visits of all non-flying vertebrates that consume* P. splendens *fruits at Los Molles (Chile).*

Species	Total number of visits	Number of visits[a]	Total number of dispersed seeds	Number of dispersed seeds[a]	Proportion of seeds dispersed to each habitat		
					Under *P. splendens*	Riverbed	Open areas
				2015[b]			
Pseudolopex griseus	8	0.17	6	0.13	0	1	0
Phyllotis darwini	8	0.17	8	0.17	0.62	0.38	0
Abrothrix olivaceus	16	0.34	4	0.08	0.75	0	0.25
Ovis sp.[c]	5	0.11	1	0.02	0	0	1
Conepatus chinga	0	0	0	0	0	0	0
Callipepla californica[c]	2	0.04	0	0	0	0	0
				2016[d]			
Pseudolopex griseus	15	0.07	2	0.01	0	0	1
Phyllotis darwini	12	0.06	3	0.01	1	0	0
Abrothrix olivaceus	3	0.01	2	0.01	0.5	0	0.5
Ovis sp.[c]	4	0.02	0	0	0	0	0
Conepatus chinga	7	0.03	0	0	0	0	0
Callipepla californica[c]	3	0.01	0	0	0	0	0
				Pooled 2015-2016			
Pseudolopex griseus	23	0.09	8	0.03	0	0.75	0.25
Phyllotis darwini	20	0.08	11	0.04	0.73	0.27	0
Abrothrix olivaceus	19	0.07	6	0.02	0.67	0	0.33
Ovis sp.[c]	9	0.03	1	0.00	0	0	1
Conepatus chinga	7	0.03	0	0	0	0	0
Callipepla californica[c]	5	0.02	0	0	0	0	0

The table shows data for frugivore visits for the 2015 and 2016 fruiting separately and for the pooled number of visits for both fruiting seasons.

[a]Per 10 h.

[b]473 h of observation.

[c]Non-native species.

[d]2165 h of observation.

removed fruits from the experimental stations; they left defleshed seeds beneath the focal plant and are thus considered solely as pulp consumers (PC; Jordano & Schupp 2000). Finally, *Ovis* sp. picked up fruits while moving and generally destroyed the seeds in the process of chewing. However, undamaged seeds occasionally fell from their mouths, resulting in some seed dispersal events; hence, it is considered as a seed predator-pulp consumer (SP-PC) (Table 1).

Except *Ovis* sp., all species handled one fruit per visit; therefore, the number of dispersed seeds per frugivore depended on the number of visits by each species ($\chi^2_{perm}(2015) = 5.97$, $P = 0.21$; $\chi^2_{perm}(2016) = 5.70$, $P = 0.63$). In 2015, we recorded a total of 39 visits, which translated into 0.82 visits per 10 h (Table 1); in 2016, this number dropped to 0.20 visits per 10-h period (44 visits in total; Table 1). The most frequent visitor to *P. splendens* varied between fruiting seasons; in 2015, the highest proportion of visits corresponded to *A. olivaceus*, whereas in 2016 it corresponded to *P. griseus* and *P. darwini* (Table 1). During the 83 visits, 94.4 percent of the fruits were handled, but 47.8 percent were not dispersed, that is, they remained beneath the canopy of the focal tree.

QUALITATIVE COMPONENT OF SEED DISPERSAL.—*Dispersal habitats.*—Over the 2 yr, 9.2 percent of the seeds were predated and 41.6 percent of the fruits were moved away from experimental stations, but only 4.1 percent were recovered (37.5% were never found). Among the dispersed fruits and seeds that were recovered, 42 percent were dispersed underneath other *P. splendens* trees (Fig. 1) and the remaining were dispersed to two other habitats: specifically, to dry riverbeds and open interspaces (Fig. 1). The frequency of seeds dispersed to each habitat differed among species in 2015 ($\chi^2_{perm} = 20.68$, $P < 0.001$); *P. griseus* dispersed seeds exclusively to riverbeds, whereas *A. olivaceus* and *P. darwini* dispersed more seeds under *P. splendens* trees. *Ovis* sp. dispersed only one seed into an open area (Table 1). In 2016, we did not record any seeds dispersed by *Ovis* sp., nor any dispersal to riverbeds; the frequency of seeds dispersed to the other two habitats did not differ among *P. griseus, A. olivaceus,* and *P. darwini* ($\chi^2_{perm} = 4.96$, $P = 0.14$).

Habitat suitability for recruitment.—Overall, the proportion of seedlings that emerged in 2015 (0.075) and 2016 (0.070) across the three habitats was very low. The mean number of emerged seedlings differed among dispersal habitats ($\chi^2 = 81.35$, df = 2,
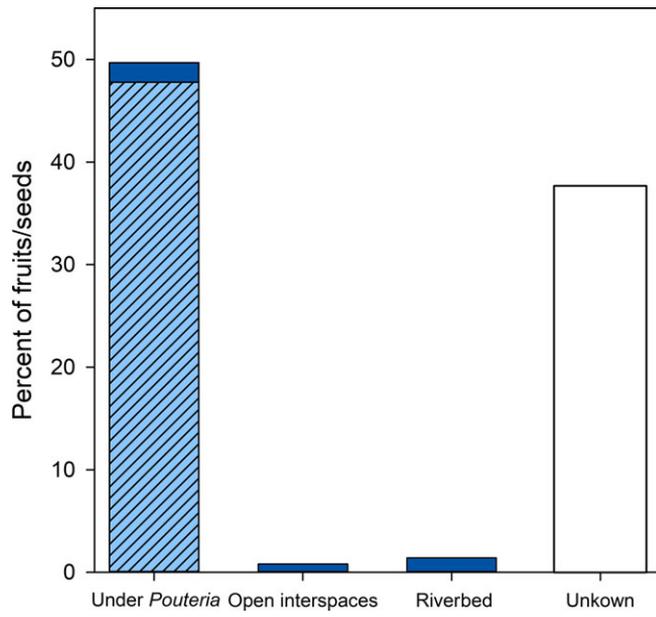
FIGURE 1. Most *Pouteria splendens* fruits/seeds from fruit experimental stations established at Los Molles (Chile) during 2015 and 2016 remained under the focal tree; few seeds were dispersed to other habitats. The light blue, hashed bar shows the percentage of fruits that were either unhandled or handled but not dispersed further than 3 m from the experimental station; the dark blue bars represent fruits/seeds that were removed more than 3 m away from the experimental station. The white bar corresponds to the percentage of fruits for which the final destination is unknown.

$P < 0.001$), but not years ($\chi^2 = 0.13$, df = 1, $P = 0.72$); moreover, there was an interaction between habitat and year ($\chi^2 = 21.31$, df = 1, $P < 0.001$). In both years, emergence was highest under conspecifics and lowest in open interspaces, but in 2016 emergence decreased under *Pouteria* and increased in riverbeds (Fig. 2A). Low and unequal samples sizes among habitats and between years precluded us from conducting statistical analyses to examine differences in seedling survival. The mean probabilities of seedling survival 12 and 20 mo after emergence are presented in Fig. 2B.

SEED DISPERSER EFFECTIVENESS.—Effectiveness was calculated only for the vertebrate species that moved fruits/seeds more than 3 m away from the focal plant on at least one occasion (*i.e.*, *P. griseus*, *P. darwini*, *A. olivaceus*, and *Ovis* sp.). The qualitative and quantitative components of *P. splendens* seed dispersal were overall low for all dispersers (Table 2; Fig. 3A); consequently, all species had very low SDE values. In both years, *P. darwini* was the species with the highest SDE, suggesting this species may be particularly important for the regeneration of *P. splendens*. Finally, our results show that SDE was context-dependent for *P. darwini* and *A. olivaceus* (Fig. 3B); effectiveness of both species decreased *ca.* sevenfold and eightfold, respectively, in 2016 compared to 2015.
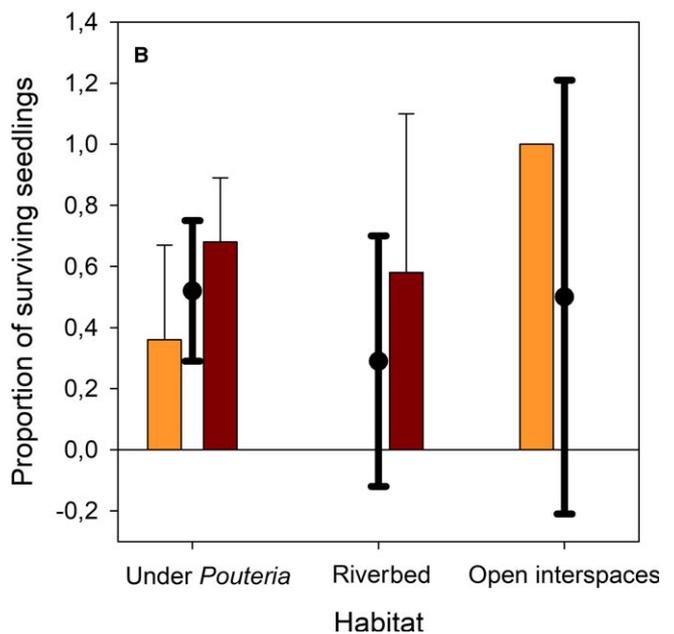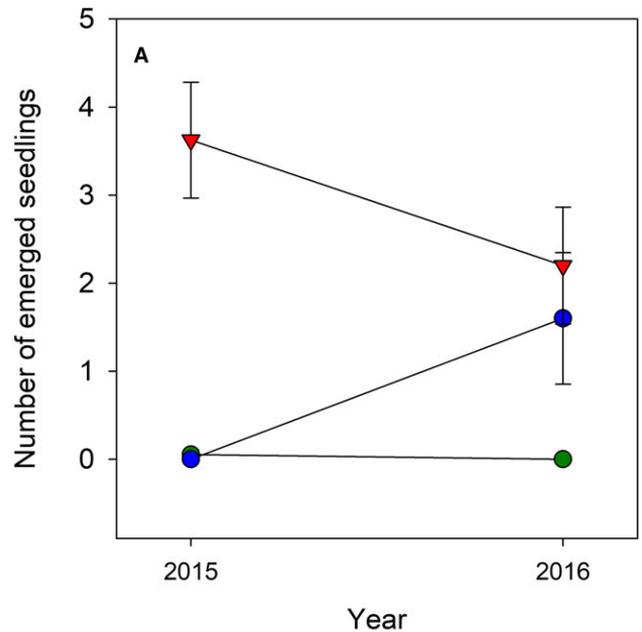

FIGURE 2. (A) Mean number (±SE) of emerged *Pouteria splendens* seedlings was higher under conspecifics (red triangles) than in riverbeds (blue circles) or open interspaces (green circles) both in 2015 and 2016. (B) Mean probability of seedling survival (±SD) in each of the habitats where *P. splendens* seeds were dispersed during 2015 (brown bars) and 2016 (orange bars) in Los Molles, Chile. Mean seedling survival (±SD) in each of the three habitats for 2015 and 2016 pooled is denoted with a circle in panel B.

DISCUSSION

Our results show that pulp consumers, which are the only present-day dispersers of *P. splendens*, appear to have very low disperser effectiveness, at least at the scales measured by our study. *P. splendens* exhibited strong dispersal limitation; most seeds were

TABLE 2. *The four species of non-flying vertebrates that dispersed* P. splendens *seeds in Los Molles (Chile) during 2015 and 2016 have very low seed disperser effectiveness (SDE) as a result of the low quantitative and qualitative components SDE.*

SDE Components	*P. griseus*	*P. darwini*	*A. olivaceus*	*Ovis* sp.
2015				
Quantitative				
Number of dispersed seeds[a]	0.13	0.17	0.08	0.02
Qualitative				
$p_e * p_s * P_d$ Under *P. splendens*	0.0000	0.0405	0.0486	0.0000
$p_e * p_s * P_d$ Riverbed	0.0000	0.0000	0.0000	0.0000
$p_e * p_s * P_d$ Open areas	0.0000	0.0000	0.0007	0.0026
$\Sigma_{(p_e * p_s * P_d)}$	0.0000	0.0405	0.0493	0.0026
SDE[a,b]	0.0000	0.0068	0.0042	0.0001
2016				
Quantitative				
Number of dispersed seeds[a]	0.01	0.01	0.01	0
Qualitative				
$p_e * p_s * P_d$ Under *P. splendens*	0.0000	0.1020	0.0510	0.0000
$p_e * p_s * P_d$ Riverbed	0.0000	0.0000	0.0000	0.0000
$p_e * p_s * P_d$ Open areas	0.0000	0.0000	0.0000	0.0000
$\Sigma_{(p_e * p_s * P_d)}$	0.0000	0.1020	0.0510	0.0000
SDE[a,b]	0.0000	0.0010	0.0005	0.0000
2015-2016				
Quantitative				
Total number of dispersed seeds[a]	0.03	0.04	0.02	0
Qualitative				
$p_e * p_s * P_d$ Under *P. splendens*	0.0000	0.0624	0.0572	0.0000
$p_e * p_s * P_d$ Riverbed	0.0120	0.0044	0.0000	0.0000
$p_e * p_s * P_d$ Open areas	0.0003	0.0000	0.0004	0.0000
$\Sigma_{(p_e * p_s * P_d)}$	0.0123	0.0668	0.0576	0.0000
SDE[a,b]	0.0004	0.0027	0.0012	0.0000

SDE for each frugivore was calculated for each year separately, as well as for both years combined (mean SDE).

[a]Per 10 h.

[b]Quantitative component * Σ of qualitative components.

p_e is probability of seedling emergence.

p_s is probability of seedling survival.

P_d is the proportion of seeds dispersed in a given microhabitat.

either left under the parent plant or dispersed only a few meters away from it. Compared to seeds that were dispersed to other microhabitats, however, those that remained under conspecifics had the highest probability of establishment. Consequently, the lack of dispersal away from parent plants does not seem to impair short-term, local-scale recruitment of *P. splendens*. Finally, our results demonstrate the context-dependence of SDE in a semiarid environment.

QUANTITATIVE COMPONENT OF SEED DISPERSAL EFFECTIVENESS.— Dispersers of *P. splendens* had low values of the quantity component of SDE resulting from the combination of low visitation rates and that all species handled only one fruit per visit. Visitation rates to *P. splendens* (0.01–0.34 visits/10 h) are among the lowest reported in the literature. For example, compared to *Prunus mahaleb* (108–454 visits/10 h; Herrera & Jordano 1981), *Eugenia umbelliflora* (0.2–6.5 visits/10 h; Cortes *et al.* 2009), and *Dendropanax arboreus* (0.19–1.96 visits/10 h; Figueroa-Esquivel *et al.* 2009), the frequency of frugivore visits to *P. splendens* is between one and four orders of magnitude smaller, revealing that this plant is dispersal limited. In the tropics, *Pouteria* fruits/seeds are dispersed by a large assemblage of vertebrates, which include primates (Arroyo-Rodríguez *et al.* 2015), rodents (Brewer & Rejmánek 1999), tapirs (Bueno *et al.* 2013), and birds (Muller-Landau *et al.* 2008), among others. Although there is little published information of visitation or removal rates of *Pouteria* fruits, richer frugivore assemblages have been linked to higher seed removal rates (García & Martínez 2012); therefore, it is improbable that tropical *Pouteria* exhibit levels of dispersal limitation as low as what we recorded here. Low visitation rates in our system may also have resulted as a consequence of high conspecific fruit density and a highly aggregated landscape, which can increase competition among plants for frugivores and ultimately reduce visitation rates to individual trees (Saracco *et al.* 2005, Smith & McWilliams 2014).

QUALITATIVE COMPONENT OF SEED DISPERSAL EFFECTIVENESS.— Most of *P. splendens* seeds arrived o remained below a conspecific plant. Theory predicts that due to negative density-dependent processes, seeds that remain close conspecifics have lower establishment probabilities than those dispersed far from them (Janzen 1970, Connell 1971). For *P. splendens*, however, the probability of seedling emergence and 2-yr seedling establishment was highest under conspecific plants. Therefore, in our system, frugivores that consistently dispersed seeds away from conspecifics had low values of the quality component of dispersal. This effect is partly explained because, during our study, seeds that moved far from the parent plant arrived to non-suitable habitats. However, frugivores may also provide long-distance dispersal to habitats similar to those of mother plants (Carlo *et al.* 2013), in which case recruitment would be favored.

Higher establishment probabilities underneath *P. splendens* canopies may be due to intra-specific facilitation, which is a process that can promote plant establishment in stressful environments (Wied & Galen 1998, Cavieres & Peñaloza 2012, Loayza *et al.* 2017). Along its area of distribution, establishment of *P. splendens* seedlings is challenging because fruits ripen during the warm and dry summer months, when its recalcitrant seeds are prone to quickly desiccate (Peña-Egaña 2017), particularly if they are dispersed to open habitats. In this regard, Sotes *et al.* (2013) examined natural recruitment patterns of *P. splendens* and found that seedling densities were significantly higher under conspecific canopies than in adjacent open areas and proposed that *P. splendens* leaf litter may prolong seed longevity and increase germination, as well as reduce seedling desiccation rates and increase survival.
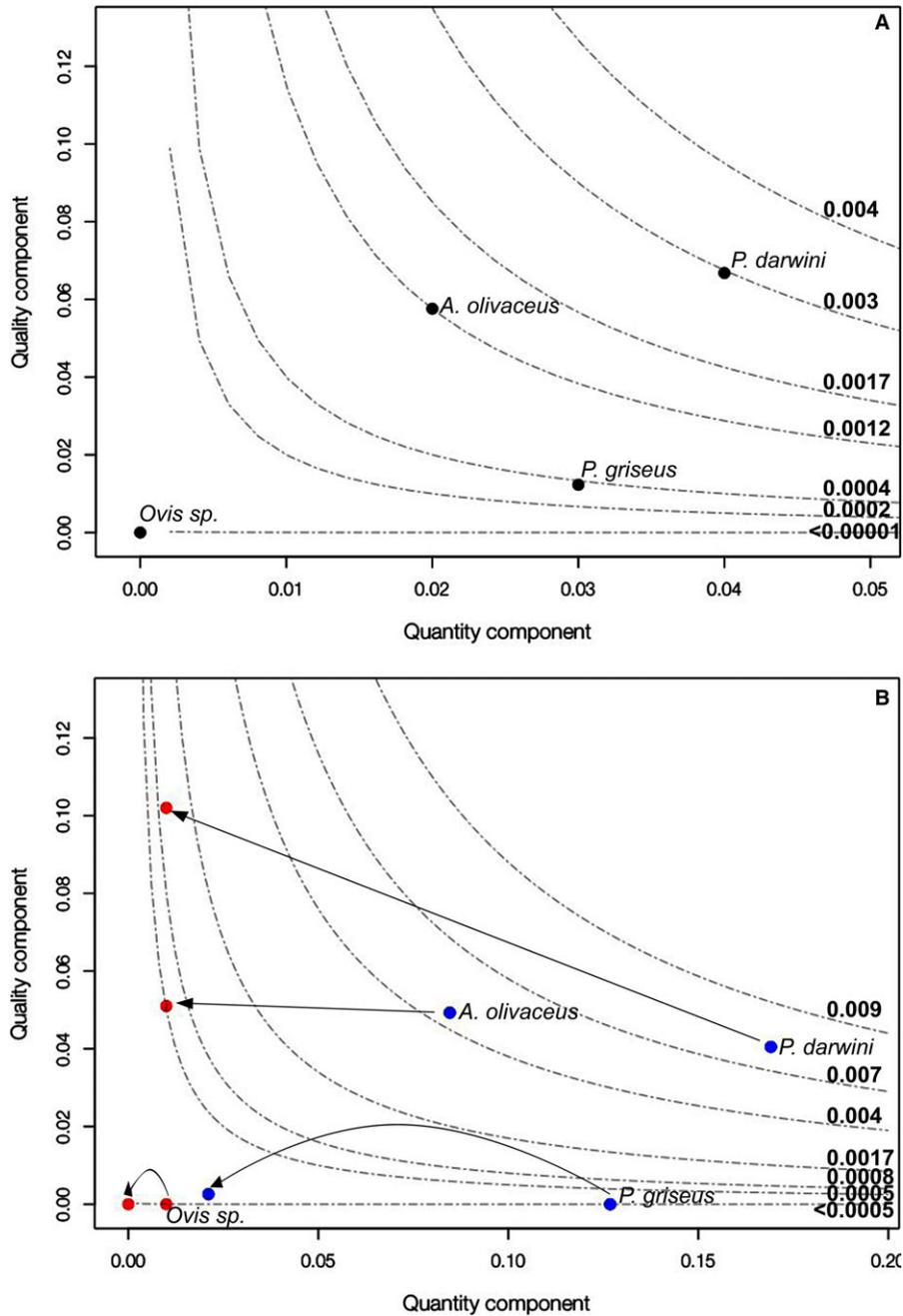
FIGURE 3. (A) Seed dispersal effectiveness (SDE) landscapes derived for the four species of non-flying vertebrates that disperse *Pouteria splendens* seeds for 2015 and 2016 combined. (B) Context-dependence of SDE revealing an overall decrease in effectiveness in 2016 (red circles) compared to 2015 (blue circles); arrows indicate the change in SDE between these years. The quantity component refers to the number of dispersed seeds per 10-h period, the quality component represents the probability that a dispersed seed produces an established seedling, and SDE is the estimated number of established seedlings produced from 10 h of dispersal activity.

We did not recover *ca.* 37 percent of the tagged fruits; however, we do not think that the fate of these seeds would alter our results for two reasons. First, as there are only four vertebrates that disperse *P. splendens* seeds at the study site (two that have small home ranges and two that generally move seeds to open habitats), it is unlikely that seeds arrive to different microhabitats

than those reported here. Nonetheless, even if this is the case, there are only a couple of microhabitats that can provide shade and leaf litter and where recruitment is feasible: under (1) *L. caustica* or under (2) *P. boldus*. In a parallel investigation at the study site, we marked >300 *P. splendens* plants across 14 randomly established plots and found no seedlings under *L. caustica* trees,

revealing that few seeds arrive to this habitat or that recruitment there is unlikely. *P. splendens* seedlings were found in a patch of sclerophyllous forest dominated by *P. boldus* and *P. splendens;* therefore, vertebrates that disperse seeds to this habitat would have higher SDE.

DISPERSER EFFECTIVENESS AND ITS CONTEXT-DEPENDENCE.—In this study, visitation frequency and the total number of dispersed seeds varied between years, adding to the empirical evidence that reveals that the quantity component of SDE is context-dependent (Schupp *et al.* 2010, Perea *et al.* 2013). Temporal variation in this component was probably driven by an intrinsic factor, namely by a 60 percent decrease in fruiting trees from 2015 to 2016 (APL, *unpublished data*), which may have temporarily decreased the strength of the interaction between *P. splendens* and its consumers. The qualitative component of SDE was relatively consistent for each species between years. This result suggests that seed treatment by vertebrates (*i.e.*, handling treatment and dispersal sites) did not change between years, and that the suitability of the dispersal habitats was also relatively constant. Indeed, in both years the 'best' habitat for recruitment was under conspecific plants. Moreover, this habitat was consistently the most suitable for both germination and seedling survival, revealing no seed-seedling conflicts in *P. splendens*' recruitment pattern (Schupp 1995).

MISSING SEED DISPERSERS AND THE FUTURE OF *P. SPLENDENS*.—Contrary to what has been observed in other systems where the absence of dispersers can lead to reduced plant recruitment (Traveset & Riera 2005, Traveset *et al.* 2012), in our system lack of seed dispersal away from parent plants may not necessarily have strong negative effects on local, short-term recruitment probabilities. Germination and seedling survival are consistently highest below conspecifics; therefore, seeds that remain in this habitat have the highest establishment probabilities. This pattern of recruitment, which deviates from the Janzen–Connell model (Janzen 1970, Connell 1971), has been found for another large-fruited/seeded tropical relict that occurs in an arid ecosystem (Loayza *et al.* 2017) and suggests that in these environments, amelioration of the harsh environmental conditions by conspecific plants to promote recruitment may compensate for the expected negative density-dependent effects of growing at high densities.

Without large-bodied vertebrates that can provide frequent effective seed dispersal services, however, *P. splendens* populations will become increasingly more isolated in light of the fact that few animals can move their seeds over large spatial scales and provide long-distance dispersal (LDD) (Pires *et al.* 2017). Without LDD, gene flow among populations can be interrupted and result in changes in the genetic structure even of relatively close populations (G. Carvallo pers. com.). Additionally, without being able to disperse their seeds over long distances, it will be difficult for plants to colonize new habitats, which when coupled with high rates of habitat loss, as is the case of *P. splendens,* results in the decrease in the distribution range of the species. Finally, although *P. splendens*' dispersers have low dispersal effectiveness, they do play one key functional role in its regeneration dynamics: They

remove the fleshy pulp from the seed, which when present significantly reduces germination probability (Peña-Egaña 2017).

We conclude that while the loss of endozoochorous seed dispersal provided by large-bodied vertebrates in unlikely to be compensated by seed dispersal from pulp consumers, the latter can still contribute to the local regeneration of large-fruited/seeded plants. Ultimately, however, long-term persistence of these plants will depend on whether they are able to adapt to dispersal by smaller vertebrates by evolving smaller fruits and seeds (Onstein *et al.* 2018).

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AUTHOR CONTRIBUTIONS

MP-E collected data, performed statistical analyses, and co-wrote the manuscript. APL collected data, performed statistical analyses, and co-wrote the manuscript; FAS contributed substantially to revisions.

DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2tn1rf9 (Peña-Egaña *et al.* 2018)

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

FIGURE S1. Species accumulation curve of non-flying vertebrates that consumed *P. splendens* fruits at Los Molles, Chile during 2015 and 2016.

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