Unusually large invasive seeds are spared by rodents in a Patagonian forest

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Abstract Seed predation by rodents can act as a recruitment barrier during community assembly, limiting the establishment of exotic species. Predation rates of exotic seeds may depend on their attractiveness, determined by their traits, and how different they are from natives. Additionally, at the naturalization stage of the invasion process, exotic seeds may escape post-dispersal predation because they are rare in the community. To test these ideas, we assessed granivory in a Patagonian forest, where two species with contrasting seed sizes are naturalized. *Rubus idaeus* seeds are of similar size of natives, whereas *Prunus cerasus* seeds are four times larger. The relative abundance of their seeds within the landscape is low compared to native seeds. Throughout the fruiting season, we offered seeds from all species present in the community (native and exotics), whenever they were available in the landscape. To consider the effects of vegetation structure on rodent foraging behavior, we offered seeds in areas with and without understory cover. We found a hump-shaped relationship between predation rates and seed size. Consequently, rodents strongly avoided large exotic *Prunus* seeds, but removed *Rubus* seeds at similar rates to natives. Contrary to our expectations, seed abundance did not affect predation, and hence, rarity did not confer an advantage to exotic seeds. The presence of shrub cover increased 2.3 times the removal rates compared to open areas. We suggest that the dissimilarity in seed size compared to native species and the presence of shrub cover influenced predation pressure on exotic species within our community.

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Introduction

In today's globalized world, the introduction of exotic species in natural habitats represents a major conservation challenge (Sala et al. 2000). Once a species arrives to a new habitat, multiple biotic and abiotic factors determine whether it thrives and becomes part

of the local community (Pearson et al. 2018; Weiher et al. 1998). Among biotic filters, post-dispersal seed predation is an important demographic bottleneck in the life cycle of plants (Crawley 2000), which can strongly affect the ability of exotic species to become part of the recipient community. Generalist granivores will impose a biotic barrier to the invasion process when consumption of exotic seeds limits their establishment and the maintenance of a self-sustained population in the new area (Pearson et al. 2014; Pearson et al. 2012). In general, granivores do not forage randomly but select seeds with certain traits that make them more profitable. They preferentially forage on species with seeds that can be handled more efficiently, provide more energy reward, nutrient content, or represent abundant food resources (reviewed in Larios et al. 2017a). Therefore, understanding which traits affect the feeding preferences of generalist granivores will improve our inferences about the potential of exotic seeds to bypass the post-dispersal predation filter in new habitats.

Among granivores, rodents are widespread generalist consumers whose foraging preferences can modulate the recruitment of exotic species (Connolly et al. 2014; Muschetto et al. 2015; Pearson et al. 2011; Maron et al. 2014). Even though factors driving rodent foraging choices can be multifaceted including coat hardness, nutrient content and phenolic compounds (Blate et al. 1998; Gong et al. 2015; Sidhu and Datta 2015), seed size is a key trait that influences their preferences (Dylewski et al. 2020). In general, seed size determines the effort needed for seed handling and the energy rewards per food item (Larios et al. 2017a; Pyke et al. 1977; Reader 1993). As a result, rodents tend to select large seeds, provided that the energetic rewards outweigh the effort needed (Lichti et al. 2017). However, the effects of seed size on granivory depend on the range of sizes present in the community. Usually, positive responses to seed size are found in small-seeded grasslands, while negative responses are common in large-seeded forests. In the former case, rodents will preferentially forage on large seeds, whereas in the latter they will select small and intermediate seed sizes (Radtke 2011). Such shifts in the response of rodents to seed size may explain the contrasting results reported in the literature, where large exotic seeds have been found to be preferentially consumed (Nuñez et al. 2008), or avoided (Pearson et al. 2011). Additionally, when

exotic seeds become part of a community, how different they are from native seeds can affect the selection by rodents. If they are dissimilar to natives with respect to key traits for rodent foraging decisions (e.g., size), exotic seeds may be perceived as a distinct food item. Consequently, they may experience differential consumption rates to those of native seeds, a pattern that has been observed in invaded communities (Pearson et al. 2014, 2018, 2011). In sum, the consumption rates of exotic seeds are expected to depend on the type of response of rodents to seed size within the recipient community (positive or negative) and on how large or small exotic seeds are with respect to natives.

In addition to species-specific characteristics like seed size, granivores may optimize their foraging by consuming the most abundant species in the seed pool (Thompson et al. 1991; Larios et al. 2017b). As central place foragers (Orians and Pearson 1979), rodents travel from their dens to feeding areas on daily basis (Morán-López et al. 2015; Rosalino et al. 2011). Under such circumstances, foraging on common "preys" (i.e., seeds) should maximize intake rates (Murdoch 1969). Since they encounter common seeds more frequently, they may be able to search and manipulate them more efficiently (reviewed in Horst and Venable 2017). Such frequency-dependent seed selection is relevant at early stages of the invasion process, when exotic species tend to show low propagule pressure, and hence, their seeds are uncommon (Křivánek et al. 2006; Pyšek et al. 2015; Simberloff 2009) and management actions can be more efficiently implemented (Simberloff et al. 2013). If rodents forage on common seeds, exotic species may benefit from being rare having a higher probability to escape post-dispersal predation. In general, studies have evaluated the positive effect of local seed abundance (i.e., density-dependent foraging) (e.g., Baraibar et al. 2012; Batisteli et al. 2020; Myster 2003; Wang 2020) while overlooking the effects of the relative abundance of seeds across the landscape (i.e., frequency-dependent foraging, Allen and Greenwood 1988).

Granivory, as any biotic interaction, can be modulated by the ecological setting in which plant-animal encounters occur. In particular, the structure of the vegetation can affect post-dispersal predation rates leading to high spatial variability in the community of recruits (Germain et al. 2013), including the

establishment of exotic species (as observed in Muschetto et al. 2022). Areas with low or no vegetation cover can reduce the activity of rodents (García et al. 2011; Kollmann and Buschor 2003), limiting the probability of seed encounter (Hulme 1994; Wang 2020). Also, it can diminish the time devoted to seed discrimination activities such as sniffing or handling seeds previous to their removal, promoting an opportunistic foraging behavior (Morán-López et al. 2018; Perea et al. 2011). Consequently, seed predation by rodents tends to be lower in open areas and the effects of seed traits on their foraging choices attenuated, equalizing seed removal rates across species. Shifts in rodent foraging behavior can alter their role in biological invasions. If they preferentially forage on exotic seeds, providing biotic resistance to the recipient community (Nuñez et al. 2008; Pearson et al. 2014), lower predation rates and selectivity in open areas could facilitate the escape of exotics from post-dispersal predation, potentially turning these areas into invasion foci. Alternatively, if rodents preferentially forage on native seeds (Pearson et al. 2011), lower activity and selectivity could facilitate the survival of natives, promoting a less invaded seedling community.

In this work, we evaluated how the foraging behavior of rodents affect the way exotic seeds integrate in the recipient community in a Patagonian temperate forest. In particular, our questions are if (1) the size of exotic seeds and how different they are from natives affected seed removal rates by rodents and if (2) rarity (i.e., low relative abundance) conferred an advantage to overcome the post-dispersal predation filter. Also, we (3) evaluated if the intensity of seed removal and selection differed between microhabitats (open areas *vs* under cover). To obtain a full picture of rodent foraging decisions, we estimated removal rates for all seeds present in the community (exotic and natives) and quantified the joint effect of seed size, relative abundances, and understory cover. In our community, two species with contrasting seed sizes, *Rubus idaeus* and *Prunus cerasus*, have become naturalized (i.e., established self-sustained populations at a considerable distance from the initial introduction but have not become dominant, Blackburn et al. 2011). Seeds of *Rubus idaeus* are of similar size to those of natives, whereas seeds of *Prunus cerasus* are four times larger than the largest native seed (Fig. 1). Seeds of both species are rare in the community, representing less

than 2.3% of seeds available across the landscape. We expected a positive effect of seed size on predation rates given that native seeds of the recipient community are small (seeds mass ranges from 2 to 33 mg). As a result, rodents would preferentially consume large *Prunus cerasus* seeds, while removing *Rubus idaeus* seeds at similar rates to natives (Reader 1993). Additionally, we expected that rodents feed on common seeds and hence, rarity would confer an advantage to exotic species. Finally, in areas with low shrub cover, we expected a lower rodent foraging activity and opportunistic foraging behavior, resulting in lower predation rates overall and subtler differences across species.

Materials and methods

Study site

The study was conducted in summer 2020 in Llao Llao Reserve within Nahuel Huapi National Park (41° 8′ S, 71° 19′ W, Río Negro, Argentina). The climate is warm and humid with a mean summer temperature of 15 °C and an average annual precipitation of 1800 mm, occurring mostly in winter (Muñoz and Garay 1985). This temperate forest is part of the Subantarctic phytogeographic province (Cabrera 1971), and vegetation structure is characterized by a mature forest interspersed with open areas. Tree canopy is dominated by *Nothofagus dombeyi* and *Austrocedrus chilensis* (Mermoz and Martin 1986), and the understory, by *Aristotelia chilensis, Azara microphylla,* and *Berberis darwinii*. Less common tree species are *Schinus patagonicus, Luma apiculata,* and *Maytenus boaria*. In the study area different fleshy-fruited exotic species have become naturalized; *Rubus idaeus*, *Prunus avium,* and *Sorbus aucuparia*. Fruit (and seed) availability peaks in summer, when almost all native and exotic species fructify (except *Luma apiculata* and *Sorbus aucuparia*). The most important seed predators in Llao Llao forest are the generalist rodents *Abrothrix hirta*, *Oligoryzomys longicaudatus*, and *Abrothix olivacea* (approximately 25 g, *Cricetidae* family) (García et al. 2011). Seed removal by granivorous birds tends to be low or absent in Patagonian temperate forests (Bravo et al. 2015) and ant granivory is negligible (according to exclusion experiments performed in the area, unpublished data).

Fig. 1 **a** Seed size of native and exotic seeds presents in the studied community (temperate Patagonian forest). **b** Relative abundance of seeds (proportion) of species present in the community across the weeks in which the cafeteria experiment was performed (from 30/01/2020 to 10/03/2020). The horizontal line in X-axis depicts the month to which each week correspond. Native seeds are represented with circles, exotics with triangles. Dots depict mean values of estimated relative abundances, whiskers 90% quantiles. In both panels note the logscale for Y-axis
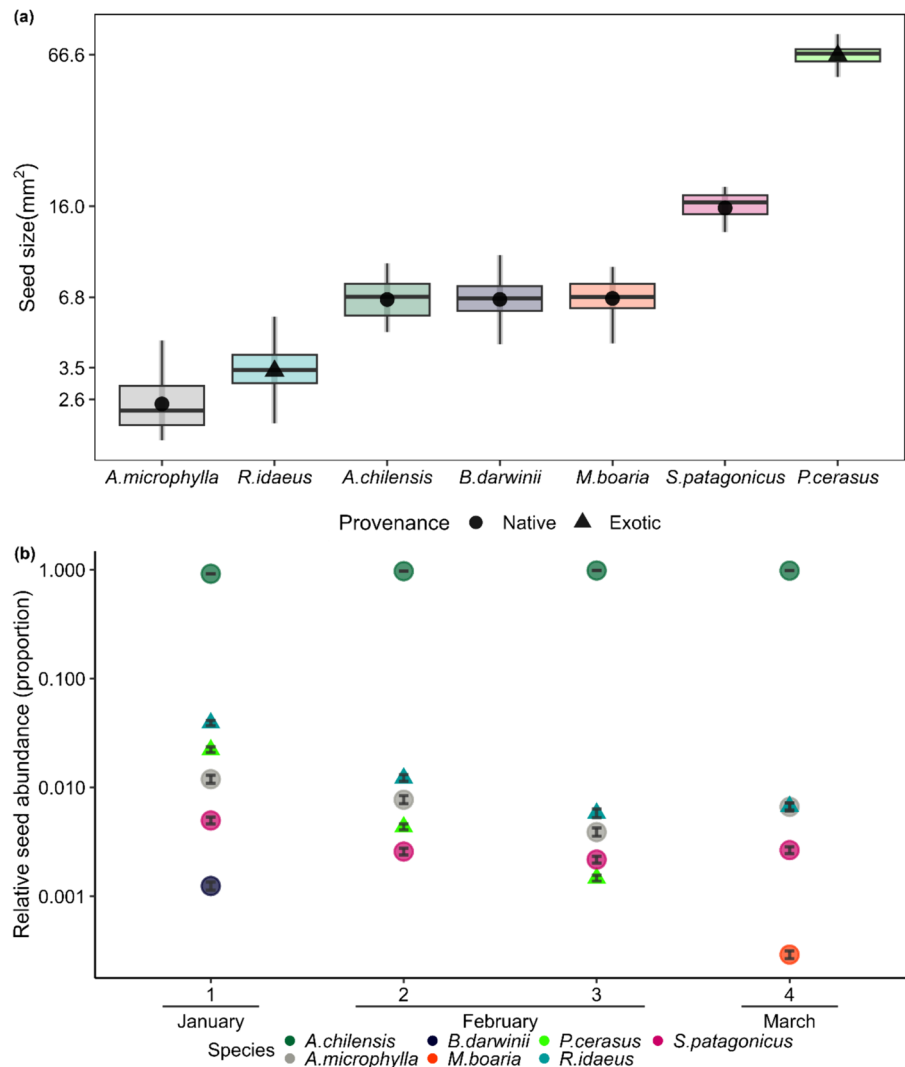
Landscape-level seed abundance

We estimated the relative abundance of seeds at the landscape-level using species-specific bootstrap samples of seed availability on a weekly basis. To this end, we combined information of the relative abundance of fruiting species, the canopy and crop size of their individuals, and their seeding phenology. To estimate species-specific relative abundances, we established 5 transects of 100×2 m comprised in an area of 10 ha, in which we identified and measured the canopy diameter of all reproductive individuals of fleshy fruited species. To estimate species-specific crop sizes, at the beginning of the fruiting season we randomly selected between 10 and 15 focal individuals of each species. We measured their canopy, counted their fruits, and marked 10 branches in which we counted the initial fruit number. On a weekly basis and for each tagged individual of each species, we monitored the number of fruits present (in branches and in the canopy) and the proportion of fruits missing in the branches (with respect to previous week). Missing fruits were mostly due to fall of ripe fruits or dispersal by birds (clean *vs* pulp remaining in the pedicel). Combining the number of fruits in branches with the proportion that went missing during the week and the number of seeds per fruit, we could infer the number of seeds of each species available to rodents in soil.

To estimate fruit availability at the landscape scale we used the approach of Carlo and Morales (2016). For each species, we estimated the number of fruiting individuals per 10 ha and randomly assigned them a canopy size according to the species-specific distribution of canopy sizes observed in transects. For instance, if the i-th plant species had 20 fruiting individuals per 10 ha, we randomly sampled 20 canopy sizes from the Gaussian kernel density estimated from the observed canopy sizes in the landscape transects. In this way, we accounted for variability in canopy sizes within species. We then estimated the crop size of sampled individuals by means of a species-specific allometric functions between canopy size and fruit production fitted to data from tagged individuals. On a weekly basis, we adjusted the number of seeds available for rodents by accounting for species-specific phenology (fruits available ripening that week) and the proportion of fruits fallen or dispersed (using data from tagged branches). Then, we converted the number of fruits into seeds considering the average number of seeds per fruit (measured in 50 fruits per species) and calculated the relative abundance of each species' seeds. This process was repeated 2000 times and the average of all replications was computed. See Supplementary material for further details.

Cafeteria experiment

To assess the combined effect of seed size of each species, their weekly relative abundance, and vegetation structure on seed removal we performed a cafeteria-style experiment (Boone and Mortelliti 2019). We selected 15 sites distributed throughout the study area (2.4 ha) harboring nearby areas with and without shrub cover. The presence of sites with such characteristics depended on tree fall gaps (Rebertus et al. 1993), which lead to a mean and minimum distance

between them of 226 m and 13 m, respectively. In each site, we established two nearby plots of 1m² located in different microhabitats: under shrub cover and in open areas. Seed-offering plots categorized as shrub cover presented > 50% of vegetation cover less than 0.5 m high (Crego et al. 2018) in a buffer of 10 m around the plot. Those categorized as open areas had no shrubs or grasses taller than 20 cm within 10 m of the plot radius. We conducted the cafeteria experiment in the peak of fruit production (four weeks, from the end of January to the middle of March of the austral summer, Lediuk et al. 2014). On a weekly basis, we offered rodents seeds of four species that were available in the landscape with two conditions: (1) they had contrasting relative abundances in the community and (2) seeds of exotic species were always present in the offering trial (Table 1). In total, 120 trials were performed (15 sites × 2 plots per site × 4 weeks). In each plot we randomly placed four wooden sticks, nailed to the soil, with 10 seeds of each species being offered (four species per trial, 40 seeds in total; Moyano et al. 2019; Motta et al. 2021). By equalizing the number of seeds per species, we isolated the effects of frequency-dependent foraging (based on the relative abundance of species at the landscape scale) from inter-specific differences in seed abundances in the offering trial (related to density-dependent effects at local scales). Seeds were glued with nontoxic odorless adhesive and manipulated with gloves to avoid human odor (Moyano et al. 2019). We monitored seed removal after 24 h, 72 h, and one week after seeds offering.

In the cafeteria experiment, we interpreted seed removal events as predation events. Rodents from the *Cricetidae* family scatter-hoard seeds with a medium weight of 0.77 g (with $q_{0.25}$ and $q_{0.75}$ ranging from 0.05 and 2.26 g, Gómez et al. 2019) a value much higher than seeds present in our community (e.g.,

Table 1 Estimated relative abundance of seeds of native and exotic species (bold type) at the landscape scale that were offered in each week of the cafeteria experiment

Week/species	A. chilensis	S. patagonicus	P. cerasus	B. darwinni	R. idaeus	A. microphylla	M. boaria
1	0.921	0.005	0.022	0.001			
2	0.973	0.003	0.004		0.012		
3	0.987	0.002			0.006	0.004	
4	0.984				0.007	0.007	0.0003

In all cases 10 seeds per species were offered (40 in total)

native seeds range between 0.002 and 0.033 g, Supplementary material, Table S1). The only exception is *Prunus cerasus* whose seed size (0.46 g) is within the range of scatter-hoarding by *Cricetidae* rodents.

Regarding seed traits, species-specific seed mass (g) and seed size (as seed area, mm^2) were calculated in 50 seeds per species. We measured seed mass in a laboratory scale with a precision of 0.001 g and the major and minor seed diameter with a gauge, and then we estimated the area assuming oval or spherical shapes (Supplementary material, Table S1). Both variables, seed size and mass were highly correlated across species (Pearson correlation coefficient 0.99, *p* value < 0.001).

Statistical analysis

Effects of shrub cover on plot encounter and seed removal

To estimate the degree of rodent foraging activity in the study area, we evaluated the effect of microhabitat (open areas *vs* shrub cover) on plot encounter probability (Hulme 1994; Wang 2020). To this end, we fitted a Bernoulli Generalized Linear Mixed Model (GLMM; logit link function) to the occurrence of seed removal in the first 24 h after offering, when differences across plots were largest (1 = at least one seed of any species was removed; 0 = no seed removal; Supplementary material 3.1). We included microhabitat as a categorical predictor (open *vs* under cover) and site as a random factor in the intercept to account for site-specific spatial variability in rodent foraging activity (e.g., due to the presence of core areas of home ranges, Rader and Krockenberger 2006), or differences in local seed availability (Fraschina and Knight 2009). In addition to plot encounter, rodents may spend more time removing seeds in microhabitats with shrub cover, which offers them shelter from predators. As a result, seed removal rates (i.e., number of seeds removed out of those offered) tends to be higher under shrub cover than in open areas (Perea et al. 2011). Consequently, to test the effect of microhabitat on seed removal rates, we performed a Generalized Linear Mixed Model (GLMM) with a binomial response (logit link, Supplementary material). We modeled the proportion of seeds removed 72 h after being offered in each plot as a function of the microhabitat where it was located (open areas *vs* under

shrub cover) and the site was included as a random factor in the intercept. We chose 72 h because it was the time when differences across plots was the largest (plots were encountered and not depleted).

Both models were fitted in a Bayesian approach, using the brms R package (Bürkner 2017). We used weakly informative priors for the intercept and sigma (random effect standard deviation), and a flat improper prior for the shrub effect term. We ran 3 chains over 10,000 iterations, leaving 1000 for warmup. After checking for convergence (Rhat < 1.01) and sufficient effective sample sizes (n.eff > 2500), we assessed model fit by means of posterior predictive checks (Supplementary material, Fig. S1-S2). See Supplementary material for full model specifications.

Factors driving foraging choices by granivores

We assumed that the number of seeds removed by each species (in each week, and plot) followed a Wallenius' hypergeometric distribution (Fog 2008), which models selection in a multivariate manner, considering the number of seeds available of each species in the offering trial. Although a multinomial distribution is frequently assumed to model data from cafeteria experiments (Boone and Mortelliti 2019; Mortelliti et al. 2019), a hypergeometric distribution considers sampling without replacement, allowing to relax the assumption that food items are refilled after each visit, which was not the case in our experimental design as seeds were not replaced after predation. We modelled seed selection probability (multinomial logit link function) as a function of the species-specific seed size (with a quadratic effect to account for possible hump-shaped responses, Dylewski et al. 2020), their relative abundance in the landscape (frequency-dependent effects), and the interaction of both covariates with shrub cover (Supplementary material). In this analysis, we used data from the 72 h revisions to avoid excess of zeros due to lack of encountering at 24 h or depletion after a week. Seed size and relative abundance showed skewed distributions, and hence, to attain a more robust model parameterization we log-transformed them. In addition, we standardized these variables (mean = 0, sd = 1) to make the magnitude of their effects comparable. We used a Bayesian approach, evaluating the likelihood function with the BiasedUrn R package (Fog 2022), and sampling the posterior distribution with a random walk

Metropolis algorithm, as implemented in the mcmc R package (Geyer 2022). We used weakly informative priors for all parameters. We ran 3 chains over 200,000 iterations, saving a sample every 20 iterations. After checking for convergence (Rhat < 1.01) and effective sample sizes (n.eff > 9000), we assessed model fit by means of posterior predictive checks (Supplementary material, Fig. S3). From posterior distributions we calculated mean effects and credible intervals (q0.025, q0.975). For specifications of priors, model structure and distributions see Supplementary material. For all regressions, we checked for spatial autocorrelation in residuals using the Moran's test ("DHARMa" package in R) (Hartig 2022). We obtained a p value > 0.05, which suggests the absence of spatial autocorrelation between sites (Supplementary material, Fig. S4, Table S2).

Results

In our community, seeds of native species tend to be relatively small (seed area ranged between 2.57 and 15.95 mm^2 and mass between 0.002 and 0.033 g, Supplementary material, Table S1). Seeds of *Rubus idaeus* are of similar size to natives, whereas those of *Prunus cerasus* much larger than the largest native (i.e., *Schinus patagonicus*) (Fig. 1a; 4 and 13 times larger with respect to seed area and weight). During the cafeteria experiment, the relative abundances of species at the landscape scale was highly variable (Fig. 1b) with seeds of *Aristotelia chilensis* dominating the community (on average representing 96% of seeds available). Relative abundance of seeds of the rest of native species ranged between 0.02 and 0.7%. In the case of *Rubus idaeus* and *Prunus cerasus* the relative abundance of their seeds was 1.58 and 0.70% across the season.

As expected, the probability of seed encountering by rodents was higher under shrub cover than in open microhabitats (Table 2). On average, after 24 h of seed offering, 55% of plots located under shrub cover were encountered, whereas this value dropped to 30% in open areas (Fig. 2a). Similarly, seed removal rates were almost 4 times higher in plots under shrub cover than in open areas (19% and 5%, covered and open respectively) (Fig. 2b).

Contrary to our expectations, within the range of seed sizes present in our community, we detected a positive effect of seed size that reversed for larger seeds (as indicated by the negative effect of the quadratic term, Table 3). Accordingly, we observed a hump-shaped response of seed removal rates of species with respect to their seed size (Fig. 3. Also, we found no effect of the relative abundance of seeds at the landscape scale (Table 3). Furthermore, foraging decisions by rodents were similar between open areas and shrub cover (non-significant interaction term of cover with seed size or relative abundance, Table 3). When comparing exotic species with natives, removal rates of *Rubus idaeus* were comparable to average values of seed removal for native species (95% quantile overlapped average values of natives), whereas removal of *Prunus cerasus* seeds were 5 times lower

Table 2 Summary of models assessing the effect of microhabitat (open areas *vs* shrub cover) on seed removal rates

	Parameter	Mean	CI	f	$\hat{R}$	n.eff
Probability of encounter						
Intercept (Shrub cover)	β_0	0.22	− 0.30; 0.80	0.78	1.00	2855
Microhabitat (Open)	β_1	**− 1.10**	**− 1.88; − 0.35**	**0.99**	**1.00**	**2799**
Site (random effect)	σ_0	0.25	0.01; 0.75	1	0.99	2675
Removal rates						
Intercept (Shrub cover)	β_0	− 1.49	− 1.91; − 1.11	1	1.00	2669
Microhabitat (Open)	β_1	**− 1.45**	**− 1.71; -1.22**	**1**	**1.00**	**2713**
Site (random effect)	σ_0	0.60	0.36; 1.06	1	1.00	2574

Probability of plot encountering during the first 24 h after seeds offering (Bernoullli regression) and seed removal rates after 72 h (Binomial regression). The site where the seed-offering plot was located was introduced as a random effect in the intercept (standard deviation across sites, σ_0). The type of microhabitat was introduced as a fixed effect, comparing open area plots (β_1) against those with shrub cover (intercept, β_0). Mean posterior distribution (mean effect), 95% credible interval (CI), proportion of the posterior with the same sign as the mean (f), Rhat ($\hat{R}$), and the effective sample size (n.eff). In bold covariate effects with f > = 0.95

Fig. 2 **a** Proportion of plots with seed removal after 24 h of seed offering located in covered or open microhabitats. Bars represent the mean values and lines the standard error (across weeks). Dots depicts mean encounter rates per week. **b** Seed removal rates after 72 h with respect to microhabitat (cover and open). In **b** dots represent removal rates per plot and week
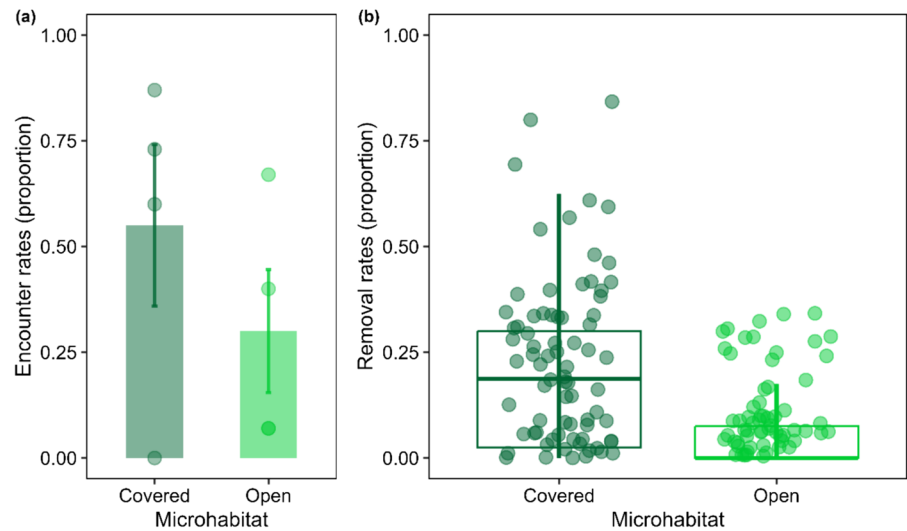
Table 3 Summary of the seed selection model according to species-specific size of seeds, their relative abundance in the landscape (frequency-dependent effects), and the type of microhabitat where the plot was located (open *vs* shrub cover, with the latter as the reference category)

	Parameter	Mean	CI	f	$\hat{R}$	n.eff
Seed size	β_1	**1.99**	**1.08, 2.91**	**0.99**	**1.00**	**16,842**
Seed size^2	β_2	**− 2.07**	**− 2.94, − 1.30**	**1**	**0.99**	**18,219**
Abundance	β_3	0.00	− 1.64, 1.64	0.50	0.99	10,300
Seed size × Microhabitat (open)	β_4	0.44	− 0.70, 1.59	0.73	0.99	14,884
Seed size^2 × Microhabitat (open)	β_5	− 0.59	− 1.86, 0.55	0.70	0.99	14,507
Abundance × Microhabitat (open)	β_6	0.01	− 1.64, 1.63	0.50	1.00	9856

Mean posterior distribution (mean effect), 95% credible interval (CI), proportion of the posterior distribution with the same sign as the mean (f), Rhat ($\hat{R}$), and effective posterior sample size (n.eff). In bold covariate effects with f > =0.95

than that of natives (0.04 vs 0.18; Fig. 4, see in Fig S5 raw values). In fact, predation rates of *Prunus* drove the hump-shaped response of predation rates to seed size (Fig. 3b).

Discussion

The selective foraging of granivores can act as a biotic filter that affects the composition of seed communities. In particular, rodent foraging preferences for certain seeds can be based on their relative abundance, their traits, as well as the environment in which they encounter them (Germain et al. 2013; Lichti et al. 2017). In the context of biological invasions, the way granivores interact with exotic seeds

can modulate how they integrate into the recipient community (Larios et al. 2017a).

During the first stages of the invasion process, exotic species establish self-sustained populations but do not become dominant in the community. As a result, propagule pressure (and the relative abundance of seeds) tends to be low (Simberloff 2009). In our community, exotic seeds of *Prunus* and *Rubus* represented together less than 2.3% of seeds available throughout the season. Rodents, as generalist foragers, are expected to focus on common seeds to increase their intake rates (Horst and Venable 2017). Hence, we posited that exotic seeds could benefit from low predation pressures given their rarity in the community. However, we found no effect of the relative abundance of seeds on removal rates (Table 3), indicating that rarity does not provide any advantage

Fig. 3 a Seed removal rates as a function of seed size in covered and open micro-habitats. Dark dots and line depict the mean and 90% credible interval predicted by the full Hypergeometric model (i.e., all covariates, Table 3). Native and exotic species are represented with circles and triangles, respectively. Asterisks represent mean observed values, and empty dots raw data. **b** Model estimates of the probability of seed removal as a function of seed size alone (i.e., partial predictions) according to the to the hypergeometric regression. To estimate partial predictions, we assumed that only one seed will be removed, that all species were offered with equal number of seeds, and that they had the same relative abundance at the landscape level. Line represents mean model predictions and ribbon 90% credible intervals. In both panels to improve data visualization X-axis was log-scaled
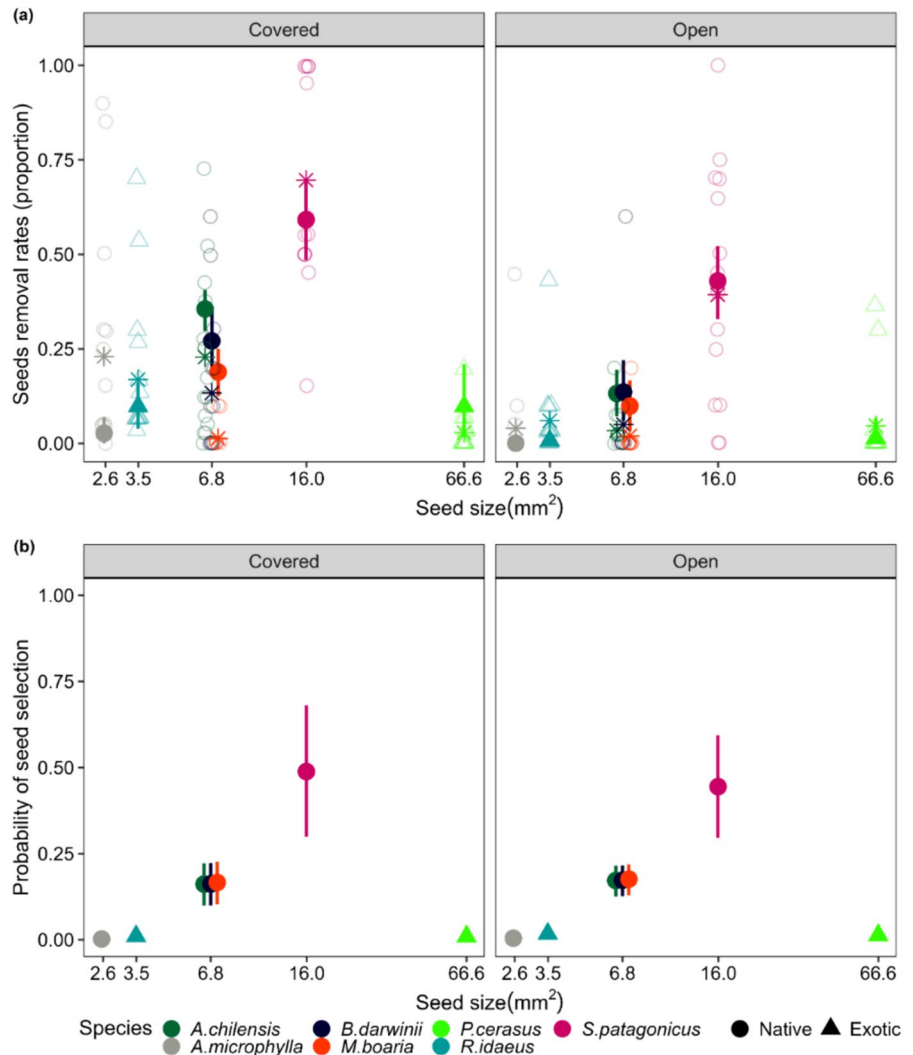
against post-dispersal predation. A possible cause of such lack of response could be a mismatch between the scale at which we measured the relative abundance of seeds and that affecting rodent foraging decisions. Rodents may respond to seed availability within their home-ranges, where they usually search for food (0.5 ha, Monteverde and Hodara 2017; Valladares-gómez et al. 2020), rather than across the landscape (2.4 ha of our study area). If the distribution of seed resources is patchy, rodent foraging choices would be driven by relative abundances at seed neighborhoods rather than at the landscape scale (Ostoja et al. 2013). However, in our study area such scenario seems unlikely. *Aristotelia chilensis* dominated the seed community throughout the fruiting season across

the landscape (> 96% of seeds available) (Fig. 1b), but showed low removal rates (0.13 ± 0.18, Fig. 4). In contrast, *Schinus patagonicus* seeds were the most preferred (0.54 ± 0.33, Fig. 4) despite being uncommon in the community (0.3% of seeds available, Fig. 1b). Such pattern suggests that in our community rodent foraging choices are driven by seed traits rather than by the relative abundance of species (see Veech 2001 for similar results).

Regarding seed traits, we found a hump-shaped relationship between predation rates and seed size (Fig. 3 Table 3). This pattern is consistent with previous studies in temperate forests, where large seed variability has been pointed out as the underlying cause of such hump-shaped responses (Dylewski

Fig. 4 Total seed removal rates by species throughout the 4 weeks of the cafeteria experiment. Native and exotic species are represented with circles and triangles, respectively. Upper panels represent removal rates in plots located under shrub cover, lower panels represent patterns in open microhabitats. Dots depict mean values (across plots throughout the season), the dark and the light lines are the [0.25–0.75] and [0.05–0.95] quantiles of the data, respectively. The red line represents the mean removal rates of native species. Observed seed removal rates across plots throughout the season can be found in Fig. S5
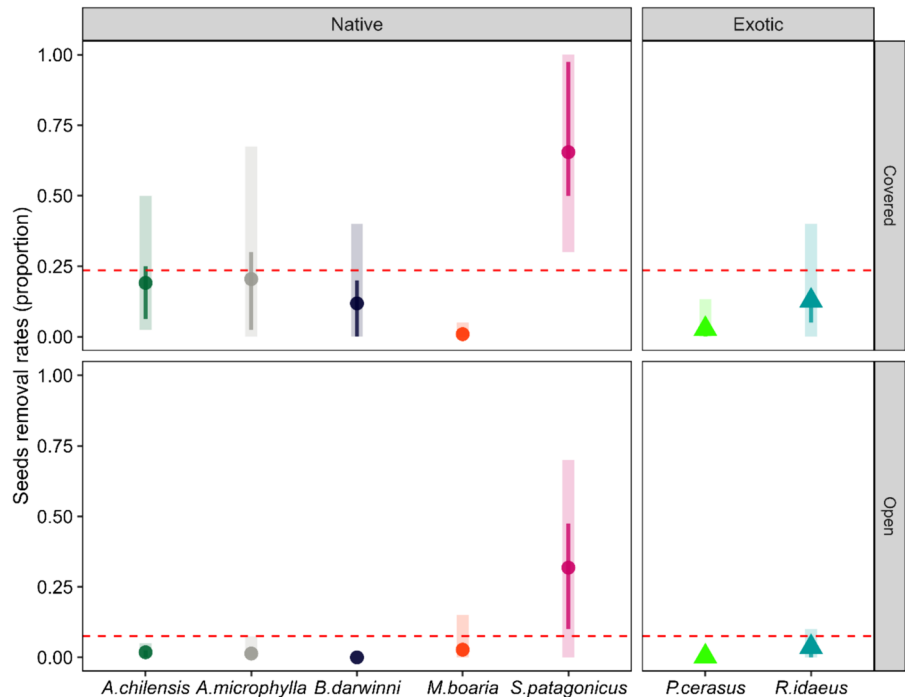
et al. 2020). However, our native community is characterized by small seeded species (12.8 mg on average), and hence, a positive response to seed size was expected (Dylewski et al. 2020). This positive response was found in the largest native seed species, but it reversed when considering the large and exotic *Prunus cerasus* seeds (Fig. 3b). Such hump-shaped response to seed size may reflect that increased handling costs of *Prunus* seeds outweigh the energetic rewards per seed item (Brewer 2001; Muñoz and Bonal 2008). In contrast, seeds of *Rubus idaeus,* which were of similar size to natives, showed average consumption rates (Figs. 1a and 4, see Connolly et al. 2014; Pearson et al. 2011 for similar results). In principle, the patterns we found can be explained by seed size effects on rodent foraging choices. The largest native seeds (*Schinus patagonicus*) were the most preferred and consumption rates of exotics matched how similar they were with respect to natives (according to Pearson et al. 2018). Nonetheless, we cannot rule out that other seed characteristics also affected seed selection. As any food item, the profitability of seeds may also depend on other traits such as coat hardness, nutrient content or toxicity (Blate et al. 1998; Kollmann et al. 1998; Lobo 2014; Gong et al. 2015; Sidhu and Datta 2015). In

this sense, *Prunus cerasus* seeds were not only the largest but their coats were harder than most natives, whereas *Rubus ideaus* seeds were similar to natives in both traits (Supplementary material, Table S1). Information of the chemical composition of seeds is partially available for exotic species, though missing for natives. Seeds of both exotic species have comparable levels of macronutrients (i.e., lipids and protein, Shaun Bushman et al 2004; Rodríguez-Blázquez et al 2023) that affect rodent foraging preferences (Kerley and Erasmus 1991; Gong et al. 2015; Morán-López et al. 2018). In addition, despite *Prunus* seeds contain chemical defenses such as cyanogenic glucosides, which are not present in *Rubus*, these compounds are not considered to be toxic for rodents (Kollman et al. 1998; Cooper and Johnson 1984). Therefore, differential removal rates of exotic seeds seem to be driven by their different sizes and not by their chemical composition. Yet, as previously acknowledged, there are significant knowledge gaps regarding the chemical composition of native seeds. Future work extending our data of seed traits will allow to evaluate if their differential removal rates mainly respond to size or a combination of characteristics. All in all, with the information available, our results support the idea that when an exotic species integrates into a

community, their similarity to natives affects the way animals interact with them, and ultimately, their probability to establish (Pearson et al. 2018).

As expected, microhabitat was a strong modulator of seed encounter and removal rates (Fig. 2). In open microhabitats seed removal rates were two times lower than under shrub cover, partly due to a reduced probability of seed encounter, a pattern previously found in the study area (García et al. 2011). However, contrary to our expectations rodent selectivity did not vary in areas with or without shrub cover (Table 3). Such pattern may reflect that predation risks in open areas within the forest were moderate, or alternatively, that rodents conducted risk-taking behaviors to ensure the removal of the highly preferred *Schinus patagonicus* seeds. Independently of the underlying cause, our results point out that the post-dispersal predation filter operates similarly across microhabitats (i.e., differences in removal rates across species were maintained), though with a lower intensity in open areas. In the context of invasions, this pattern implies low removal rates of *Prunus cerasus* seeds irrespectively of the microhabitat. At this point, it is important to note that caching of *Prunus* seeds have been reported for rodents of the *Cricetidae* family, though with low cache survival (Beck and Vander Wall 2010; Fei et al. 2011). Whether low removal rates results advantageous or not for *Prunus cerasus* will depend on the balance between seed caching and predation rates of handled seeds in our study area (Gómez et al. 2019). In the rest of species, we are confident that removed seeds were predated given their small size. Thus, our results suggest that in open areas seeds have a higher probability to survive, at least in the short term. It remains an open question if reduced predation translates into enhanced recruitment. It will depend, among others, on the suitability of environmental conditions in open areas (according to the regeneration niche of species (Grubb 1977).

Our work shows that in our community removal rates across species is highly variable and suggest that these patterns are mediated by seed size and by vegetation structure. Both factors affected how exotic seeds interacted with rodents in the recipient community and, ultimately, post-dispersal seed removal rates. In particular, *Prunus cerasus* seeds, which were 4 times larger than the largest natives, were systematically avoided, whereas those of *Rubus idaeus* were removed at similar rates to them (Figs. 1a and 4).

These results support the idea that the performance of exotic species in a new community will depend on how different they are from natives (Pearson et al. 2018) and agrees with the notion that seed size is an important factor influencing the foraging choices of rodents (Dylewski et al. 2020; Radtke 2011). Regarding vegetation structure, even though seed selection patterns were consistent across microhabitats, in open areas seeds had two times higher probability of not being removed than under shrub cover. Given the small size of seeds in our community, we expected that seed removal would mostly reflect predation rates. Thus, our results suggest that in our community seeds located in open areas have a higher probability to bypass the post-dispersal predation filter.

Declarations

References

Allen JA, Greenwood JJD (1988) Frequency-dependent selection by predators. Philos Trans R Soc Lond Ser B Biol Sci 319:485–503

Baraibar B, Daedlow D, De Mol F, Gerowitt B (2012) Density dependence of weed seed predation by invertebrates and vertebrates in winter wheat. Weed Res 52:79–87

Batisteli AF, Email B, Washington R, Jo R (2020) Seed abundance affects seed removal of an alien and a native tree in the Brazilian savanna: implications for biotic resistance. Austral Ecol 45:1–9. https://doi.org/10.1111/aec.12922

Beck MJ, Vander Wall SB (2010) Seed dispersal by scatter-hoarding rodents in arid environments. J Ecol 98:1300–1309. https://doi.org/10.1111/j.1365-2745.2010.01716.x

Blackburn TM et al (2011) A proposed unified framework for biological invasions. Trends Ecol Evol 26(7):333–339

Blate G et al (1998) Post-dispersal predation on isolated seeds: a comparative study of 40 tree species in a Southeast Asian rainforest. Oikos 82(3):522–538. https://doi.org/10.2307/3546373

Boone SR, Mortelliti A (2019) Small mammal tree seed selection in mixed forests of the Eastern United States. For Ecol Manage 449:117487. https://doi.org/10.1016/J.FORECO.2019.117487

Bravo SP, Cueto VR, Amico GC (2015) Do animal–plant interactions influence the spatial distribution of *Aristotelia chilensis* shrubs in temperate forests of southern South America? Plant Ecol 216:383–394

Brewer S (2001) Predation and dispersal of large and small seeds of a tropical palm. Oikos 92(2):245–255

Bürkner P (2017) brms: an R package for Bayesian multi-level models using Stan. J Stat Softw 80:1–28. https://doi.org/10.18637/jss.v080.i01

Bushman BS, Phillips B, Isbell T, Ou B, Crane JM, Knapp SJ (2004) Chemical composition of caneberry (Rubus spp.) seeds and oils and their antioxidant potential. J Agric Food Chem 52(26):7982–7987. https://doi.org/10.1021/jf049149a

Cabrera AL (1971) Sociedad Argentina de Botánica. Boletín de la Sociedad Argentina Botánica 14:1–50

Carlo TA, Morales JM (2016) Generalist birds promote tropical forest regeneration and increase plant diversity via rare-biased seed dispersal. Ecology 97(7):1819–1831. https://doi.org/10.1890/15-2147.1HKK

Connolly BM, Pearson D, Mack RN (2014) Granivory of invasive, naturalized, and native plants in communities differentially susceptible to invasion. Ecology 95:1759–1769

Cooper MR, Johnson AW (1984) Poisonous plants in Britain and their effect on animals and man. Her Majesty's Stationery Office, London

Crawley MJ (2000) Seed predators and plant population dynamics. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities. Cabi, Wallingford, pp 167–182

Crego RD, Jiménez JE, Rozzi R (2018) Macro- and micro-habitat selection of small rodents and their predation risk perception under a novel invasive predator at the southern end of the Americas. Mamm Res 63:267–275. https://doi.org/10.1007/s13364-018-0361-5

Dylewski L, Ortega KY, Bogdziewicz M, Pearson ED (2020) Seed size predicts global effects of small mammal seed predation on plant recruitment. Ecol Lett 23:1024–1033. https://doi.org/10.1111/ele.13499

Fei Yu et al (2011) Effect of small rodents on seed dispersal of five tree species in Xiaoxing' an Mountains. J Northeast For Univ 39:11–13

Fog A (2008) Sampling methods for Wallenius' and Fisher's noncentral hypergeometric distributions. Commun Stat Simul Comput 37(2):241–257

Fog A (2022) Biased Urn Theory. https://cran.r-project.org/web/packages/BiasedUrn/vignettes/UrnTheory.pdf

Fraschina BJ, Knight C (2009) Foraging efficiency of *Akodon azarae* under different plant cover and resource levels. J Ethol 27:447–452

García D, Zamora R, Amico GC (2011) The spatial scale of plant-animal interactions: effects of resource availability and habitat structure. Ecol Monogr 81:103–121. https://doi.org/10.1890/10-0470.1

Germain RM, Johnson L, Schneider S et al (2013) Spatial variability in plant predation determines the strength of stochastic community assembly. Am Nat 182:169–179. https://doi.org/10.1086/670928

Geyer CJ (2022) Package "mcmc". https://cran.r-project.org/web/packages/mcmc/mcmc.pdf

Gómez JM, Schupp EW, Jordano P (2019) Synzoochory: the ecological and evolutionary relevance of a dual interaction. Biol Rev 94(3):874–902

Gong H, Tang C, Wang B (2015) Post-dispersal seed predation and its relations with seed traits: a thirty-species-comparative study. Plant Species Biol 30:193–201. https://doi.org/10.1111/1442-1984.12051

Grubb PJ (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol Rev 52:107–145

Hartig F (2022) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. Theoretical Ecology, University of Regensburg. https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html

Horst JL, Venable DL (2017) Frequency-dependent seed predation by rodents on Sonoran Desert winter annual plants. Ecology 99:196–203. https://doi.org/10.1002/ecy.2066

Hulme PE (1994) Post-dispersal seed predation in grassland: its magnitude and sources of variation. J Ecol 82:645–652

Kerley GIH, Erasmus T (1991) What do mice select for in seeds? Oecologia 86:261–267

Kollmann J, Buschor M (2003) Edges effects on seed predation by rodents in deciduous forests of northern Switzerland. Plant Ecol 164:249–261

Kollmann J, Coomes DA, White SM (1998) Consistencies in post-dispersal seed predation of temperate fleshy-fruited species among seasons, years and sites. Funct Ecol 12(4):683–690

Křivánek M, Pyšek P, Jarošík V (2006) Planting history and propagule pressure as predictors of invasion by woody species in a Temperate Region. Conserv Biol 20:1487–1498. https://doi.org/10.1111/j.1523-1739.2006.00477.x

Larios E, Búrquez A, Valenzuela G et al (2017a) Post-dispersal seed predation in relation to selection on seed size in *Dithyrea californica*. Evol Ecol Res 18:651–662

Larios L, Pearson DE, Maron JL (2017b) Incorporating the effects of generalist seed predators into plant community theory. Funct Ecol 31:1856–1867. https://doi.org/10.1111/1365-2435.12905

Lediuk KD, Damascos MA, Puntieri JG, Svriz M (2014) Differences in phenology and fruit characteristic between invasive and native woody species favor exotic species

invasiveness. Plant Ecol 215:1455–1467. https://doi.org/10.1007/s11258-014-0402-3

Lichti NI, Steele MA, Swihart RK (2017) Seed fate and decision-making processes in scatter-hoarding rodents. Biol Rev Camb Philos Soc 92:474–504. https://doi.org/10.1111/brv.12240

Lobo N (2014) Conifer seed predation by terrestrial small mammals: a review of the patterns, implications, and limitations of top-down and bottom-up interactions. For Ecol Manage 328:45–54. https://doi.org/10.1016/j.foreco.2014.05.019

Maron JL, Kathryn CB, Angert AL (2014) Disentangling the drivers of context-dependent plant-animal interactions. J Ecol 102(6):1485–1496

Mermoz M, Martin C (1986) Mapa de vegetación de la Reserva y del Parque Nacional Nahuel Huapi. Administración de Parques Nacionales, Delegación Técnica Regional Patagonia. Informe Técnico. 23

Monteverde MJ, Hodara K (2017) Movimientos de roedores intra- e inter-ambiente y riesgo de exposición al Hantavirus "Andes" en Patagonia norte, Argentina. Ecol Austral 27:279–289

Morán-López T, Wiegand T, Morales JM, Valladares F, Díaz M (2015) Predicting forest management effects on oak–rodent mutualisms. Oikos 000:001–013. https://doi.org/10.1111/oik.02884

Morán-López T, Valladares F, Tiribelli F et al (2018) Fragmentation modifies seed trait effects on scatter-hoarders' foraging decisions. Plant Ecol 219:325–342. https://doi.org/10.1007/s11258-018-0798-2

Mortelliti A, Ilona PG, Shawn F et al (2019) Small mammal controls on the climate-driven range shift of woody plant species. Oikos. https://doi.org/10.1111/oik.06643

Motta L, Vitali A, Amico CG (2021) Post-dispersal seed predation in Patagonia temperate forest depends on habitat patchiness and seed species. Plant Ecol 222:819–827

Moyano J, Chiuffo MC, Nuñez MA, Rodriguez MA (2019) Seed predation does not explain pine invasion success. Oecologia. https://doi.org/10.1007/s00442-019-04354-8

Muñoz E, Garay A (1985) Caracterización climática de la provincia de Río Negro. INTA- EERA. S.C. de Bariloche. Informe técnico n° 56.

Muñoz A, Bonal R (2008) Are you strong enough to carry that seed? Seed size/body size ratios influence seed choices by rodents. Anim Behav 76(3):709–715

Murdoch WW (1969) Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol Monogr 39:335–354. https://doi.org/10.2307/1942352

Muschetto E, Mazia N, Cueto GR, Busch M (2015) Are rodents a source of biotic resistance to tree invasion in Pampean grasslands? Tree seed consumption under different conditions. Austral Ecol 40:255–266

Muschetto E, Chaneton EJ, Mazía N et al (2022) Biotic resistance in a stochastic world: do rodents act as a filter to alien tree invasion in pampean old fields? Ecol Res 37(5):568–581

Myster RW (2003) Effects of species, density, patch-type, and season on post-dispersal seed predation in a Puerto Rican pasture. Biotropica 35:542–546. https://doi.org/10.1111/J.1744-7429.2003.TB00610.X

Nuñez MA, Simberloff D, Relva MA (2008) Seed predation as a barrier to alien conifer invasions. Biol Invasions 10:1389–1398. https://doi.org/10.1007/s10530-007-9214-x

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR (eds) Analysis of ecological systems. Ohio State University Press, Columbus, OH, pp 155–177

Ostoja SM, Schupp EW, Durham S, Klinger R (2013) Seed harvesting is influenced by associational effects in mixed seed neighborhoods, not just by seed density. Funct Ecol 27:775–785

Pearson DE, Callaway RM, Maron JL (2011) Biotic resistance via granivory: establishment by invasive, naturalized, and native asters reflects generalist preference. Ecology 92:1748–1757. https://doi.org/10.1890/11-0164.1

Pearson DE, Potter T, Maron JL (2012) Biotic resistance: exclusion of native rodent consumers releases populations of a weak invader. J Ecol 100:1383–1390. https://doi.org/10.1111/j.1365-2745.2012.02025.x

Pearson DE, Hierro JL, Chiuffo M, Villarreal D (2014) Rodent seed predation as a biotic filter influencing exotic plant abundance and distribution. Biol Invasions 16:1185–1196. https://doi.org/10.1007/s10530-013-0573-1

Pearson DE, Ortega YK, Eren Ö, Hierro JL (2018) Community assembly theory as a framework for biological invasions. Trends Ecol Evol 33:313–325. https://doi.org/10.1016/j.tree.2018.03.002

Perea R, González R, San Miguel A, Gil L (2011) Moonlight and shelter cause differential seed selection and removal by rodents. Anim Behav 82:717–723

Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: selective review of theory and tests. Q Rev Biol 52:137–154

Pyšek P et al (2015) Naturalization of central European plants in North America: species traits, habitats, propagule pressure, residence time. Ecol Soc Am 96:762–774

Rader R, Krockenberger AK (2006) Use of space by a tropical rainforest rodent, *Melomys cervinipes*, and its implications for foraging and home-range size. Wildl Res 33:577–582

Radtke TM (2011) Granivore seed-size preferences. Seed Sci Res 21:81–83

Reader RJ (1993) Control of seedling emergence by ground cover and seed predation in relation to seed size for some old-field species. J Ecol 81:169–175

Rebertus AJ, Veblen TT, Kitzberger T (1993) Gap formation and dieback in Fuego-Patagonian Nothofagus forests. Phytocoenologia 23(581):599

Rodríguez-Blázquez S, Gómez-Mejía E, Rosales-Conrado N, León-González ME, García-Sánchez B, Miranda R (2023) Valorization of prunus seed oils: fatty acids composition and oxidative stability. Molecules 28(20):7045. https://doi.org/10.3390/molecules28207045

Rosalino LM et al (2011) Usage patterns of Mediterranean agro-forest habitat components by wood mice *Apodemus sylvaticus*. Mamm Biol 76:268–273

Sala OE et al (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774. https://doi.org/10.1126/science.287.5459.1770

Sidhu S, Datta A (2015) Tracking seed fates of tropical tree species: evidence for seed caching in a tropical forest in north-east India. PLoS ONE 10:e0134658

Simberloff D (2009) The role of propagule pressure in biological invasions. Annu Rev Ecol Syst 40:81–102. https://doi.org/10.1146/annurev.ecolsys.110308.120304

Simberloff D, Martin JL, Genovesi P, et al (2013) Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol 28:58–66

Thompson DB, Brown JH, Spencer WD (1991) Indirect facilitation of granivorous birds by desert rodents: experimental evidence from foraging patterns. Ecology 72:852–863

Valladares-gómez B et al (2020) Morphological variation in two sigmodontine rodents along the mainland and the Fuegian archipelago in Chilean southern Patagonia. Rev Chil Hist Nat 93:2–12

Veech JA (2001) The foraging behavior of granivorous rodents and short-term apparent competition among seeds. Behav Ecol 12:467–474

Wang B (2020) Seed density affects post-dispersal seed predation: evidence from a seed removal experiment of 62 species. Integr Zool 152:135–143. https://doi.org/10.1111/1749-4877.12421

Weiher E et al (1998) Community assembly rules, morphological dispersion, and the coexistence of plant species. Oikos 81:309–322. https://doi.org/10.2307/3547051