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

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Research Article

Keywords: granivory, seed size, landscape abundance, exotic species, shrub cover

Posted Date: December 20th, 2023

DOI: https://doi.org/10.21203/rs.3.rs-3486331/v1

Version of Record: A version of this preprint was published at Biological Invasions on June 18th, 2024.
See the published version at https://doi.org/10.1007/s10530-024-03372-9.

Abstract

Seed predation by rodents can act as a barrier, 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 uncommon 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 to native species, 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 or without understory cover. Seed size affected the probability of removal, with rodents preferentially foraging on those of intermediate sizes. Consequently, they strongly avoided large *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. Concluding, the dissimilarity in seed size compared to native species and the presence of shrub cover influenced the predation pressure on exotic species within our community.

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 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, Potter and Maron 2012). In general, granivores do not forage randomly but select seeds with certain characteristics 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. 2017). 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). Even though factors driving rodent foraging choices can be multifaceted (e.g., coat hardness, nutrient content, phenolic compounds (Blate et al. 1998; Gong, Tang, and Wang 2015; Sidhu and Datta

2015)), seed size is a key trait that influences their eating preferences (Dylewski et al. 2020). In general, seed size effects are not unequivocal but 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 (Radtke 2011). Such shifts in the response to seed size may explain the contrasting results reported in literature, where large exotic seeds have been found to be preferentially consumed (Nuñez, Simberloff, and Relva 2008), or avoided (Pearson, Callaway, and Maron 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 new food item, and hence, show differential consumption rates to those of native seeds (Pearson et al. 2018), a pattern that has been observed in invaded communities (Pearson et al. 2014; Pearson et al. 2018; Pearson, Callaway, and Maron 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, Brown, and Spencer 1991; Larios, Pearson, and Maron 2017). Such positive density-dependent foraging has been mainly tested at local scales and is explained by the attraction of rodents towards areas with abundant seeds (e.g., Baraibar et al. 2012; Batisteli et al. 2020; Myster 2003; Wang 2020). In contrast, the effect of relative seed abundance at landscape and community scales has been ignored even though it could impact predation rates over exotic seeds. At early stages of the invasion process, exotic species tend to show low propagule pressure (Křivánek, Pyšek, and Jarošík 2006; Pyšek et al. 2015; Simberloff 2009). Thus, if rodents forage on common seeds, exotic species may benefit from being rare. From an applied standpoint, this can be particularly relevant as it is at early stages of the invasion process when management actions can be more efficiently implemented (Simberloff et al. 2013).

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 lack of vegetation cover (e.g., shrubs) can reduce the activity of rodents (García, Zamora, and Amico 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, promoting an opportunistic foraging behavior (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. If rodents preferentially consume exotic seeds, such shifts in rodent foraging behavior can decrease predation pressures on them (i.e., they would be encountered less often and seed selection attenuated). Under such circumstances, biotic resistance would be relaxed in open areas potentially turning them into invasion foci.

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 (i) the size of exotic seeds and how different they are from natives affected seed removal rates by rodents and if (ii) rarity conferred an advantage to overcome the post-dispersal predation filter. Also, we 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 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 rarity to confer an advantage to exotic species, since a positive response to local seed abundance has been previously observed in the area (García, Zamora, and Amico 2011). Finally, in areas with low shrub cover, we expected a lower rodent foraging activity and a more opportunistic foraging behavior, resulting in lower predation rates 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 (41º8’ S, 71º19’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, Zamora, and Amico 2011). Seed removal by granivorous birds tends to be low or absent in Patagonian temperate forests (Bravo, Cueto, and Amico 2015) and ant granivory is negligible (according to exclusion experiments performed in the area, unpublished data).

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 x 2 m 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, we could infer the number of fruits present in the soil and available for rodents. To estimate fruit availability at the landscape scale we followed Carlo and Morales (2016). For each species we sampled with replacement a number of individuals equal to the number of fruit producer individuals per 10 ha and assigned them a canopy size (according to observed values in transects). We then estimated the crop size of sampled individuals by means of a species-specific allometric function 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) with a mean and minimum distance between them of 226 m and 13 m, respectively. In each site, we established two nearby plots 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 meter high (Crego, Jiménez, and Rozzi 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 end of February 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: (i) they had contrasting relative abundances and (ii) seeds of exotic species were always present in the offering trial (Supplementary material, Table S2). In total, 120 trials were performed (15 sites x 2 plots per site x 4 weeks). In each plot we randomly placed four wooden

sticks, nailed to the soil, with 10 seeds of a single species (four species per trial, 40 seeds in total) (Moyano et al. 2019, Motta et al. 2021). By offering the same number of seeds per species in each trial, we ensure that the relative abundance of seeds varies only at the landscape scale, thus avoiding confounding effects. 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, Schupp, and Jordano 2019) a value much higher than seeds present in our community (e.g., native seeds range between 0.002 to 0.033 g, and seeds of all species except for *Prunus* weight less than 0.05 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. In fact, seed caching by *Cricetidae* rodents have been previously reported (Beck and Wall 2010; Yu Fei et al. 2011). However, cache survival tends to be low reflecting that rodents mainly act as seed predators having negative values in the mutualism-antagonism continuum (Gómez, Schupp, and Jordano 2019).

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 0.001g 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 hours after offering, when differences across plots were largest (1 = at least one seed of any species was removed; 0 = no seed removal; Supplementary material). 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 tend 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 hours after seeds 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.

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 4 and 3 chains (respectively) over 10000 iterations, leaving 1000 for warm-up. 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 modeled seed selection by rodents as a function of species-specific seed size, their weekly relative abundance and the type of microhabitat of seed-offering plots (open areas *vs* under cover). We assumed that the number of seeds removed by each species, among those available, each week, and in each plot (response variable) followed a (multivariate) Wallenius' hypergeometric distribution (Fog 2008), which models seeds selection in a multivariate manner, considering the number of seeds available per species in each foraging event. This is an appropriate approach when different types of resources are available. 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 met 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, 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. 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 200000 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 model residuals using the Moran's test ("DHARMa" package in R) (Hartig 2022). We obtained a Moran's Index of 0.21 with a p-value of 0.14 which suggests the absence of spatial autocorrelation between sites.

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 ideaus* 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 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 was1.58 and 0.93% across the season.

As expected, the probability of seed encountering by rodents was higher under shrub cover than in open microhabitats (Table 1). On average, after 24 h of seed offering 73% of plots located under shrub cover were encountered, whereas this value dropped to 40% 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).

Table 1
Summary of models assessing the effect of microhabitat (open areas *vs* shrub cover) on seed removal rates. Probability of plot encountering during the first 24 hours 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 ($\widehat{\mathrm{R}}$), and the effective sample size (n.eff). In bold covariate effects with f > = 0.95.

	Parameter	Mean	CI	f	$\widehat{\mathrm{R}}$	n.eff
Probability of encounter						
Intercept (Shrub cover)	β_0	1.27	-0.03; 2.92	0.96	1.00	3548
Microhabitat (Open)	β_1	**-1.80**	**-3.77; -0.16**	**0.98**	**1.00**	**3598**
Site (random effect)	σ_0	0.99	0.03; 2.88	1	0.99	3578
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

Regarding seed selection by granivores, we detected a positive effect of seed size that reversed for seeds larger than 20 mm^2 or 33 mg (as indicated by the negative effect of the quadratic term, Fig. 3b, Table 2). Accordingly, we observed a hump-shaped response of seed removal rates of species with respect to their seed size (Fig. 3a). Contrary to our expectations, we found no effect of the relative abundance of seeds at the landscape scale (Table 2). Also, we found that foraging decisions of rodents were similar between open areas and shrub cover (non-significant interaction term of cover with seed size or relative abundance, Table 2). 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

than that of natives (which removal rates are 0.04 and 0.18, respectively; Fig. 4). In fact, predation rates of *Prunus* drove the hump-shaped response of predation rates to seed size (Fig. 3a).

Table 2
Summary of the seed selection model according to species-specific size of seeds, their relative abundance in the landscape, and the type of microhabitat where the plot was located (open *vs* shrub cover, with the latter as the reference category). Mean posterior distribution (mean effect), 95% credible interval (CI), proportion of the posterior distribution with the same sign as the mean (f), Rhat $(\widehat{\mathrm{R}})$, and effective posterior sample size (n.eff). In bold covariate effects with f > = 0.95.

	Parameter	Mean	CI	f	$\widehat{\text{varvec}R}$	n.eff
Seed size	β_1	**1.99**	**1.08, 2.91**	**0.99**	**1.00**	**16842**
Seed size^2	β_2	**-2.07**	**-2.94, -1.30**	**1**	**0.99**	**18219**
Abundance	β_3	0.00	-1.64, 1.64	0.50	0.99	10300
Seed size × Microhabitat (open)	β_4	0.44	-0.70, 1.59	0.73	0.99	14884
Seed size^2 × Microhabitat (open)	β_5	-0.59	-1.86, 0.55	0.70	0.99	14507
Abundance × Microhabitat (open)	β_6	0.01	-1.64, 1.63	0.50	1.00	9856

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, Steele, and Swihart 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. 2017).

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 tends to be low (Simberloff 2009). Under such circumstances and in areas where rodents are the most important seed predators, exotic seeds may benefit from low predation pressures, since they tend to be density-dependent foragers (Baraibar et al. 2012; Daedlow et al. 2014; Myster 2003; Pardini, Patten, and Knight 2017). In our community, exotic seeds of *Prunus* and *Rubus* represented less than 3% of seeds available. However, we found no effect of relative abundance on seed removal rates (Table 2), and hence, rarity did not provide

them any advantage. 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 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), suggesting that rodents preferred intermediate-sized seeds. 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 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). Accordingly, when considering only native seed species, rodents preferred large *Schinus patagonicus* seeds. In fact, the negative effects of seed size were mainly driven by low predation rates on *Prunus cerasus* (Fig. 3a). Therefore, we believe that the hump-shaped response found here is not due to the range of seed sizes present in the recipient community, but to the avoidance of *Prunus cerasus* seeds by rodents. Probably, *Prunus cerasus* seeds were under-consumed in response to their increased handling costs due to their large size (Brewer 2001; Muñoz and Bonal 2008). However, we cannot dismiss other characteristics of seeds, like higher coat thickness and hardness than the native species (Supplementary material, Table S1). Irrespectively of the seed trait, 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). In this line, *Rubus idaeus*, with seeds of similar size to those of natives, showed average consumption rates (Fig. 1a and 4). Similar results have been found in other invaded communities, where large exotic seeds are under-consumed and exotic seeds with size within the range of the recipient community are predated at similar rates to those of natives (e.g., Connolly et al. 2014; Pearson et al. 2011).

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, Zamora, and Amico 2011). However, contrary to our expectations rodent selectivity did not vary in areas with or without shrub cover (Table 2). 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. Whether such pattern results advantageous or not will depend on the balance between seed caching and predation rates of handled seeds (Gómez, Schupp, and Jordano 2019). From a community perspective, our results suggest that in open areas seeds have a higher probability to survive predation, 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).

Overall, our work shows that in our study system the probability of seed removal by rodents is mediated by species-specific seed size and vegetation structure. Such patterns affected how exotic seeds interacted with rodents in the recipient community. 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 (Fig. 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 confirms seed size as 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 remaining unremoved 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

Acknowledgements

Mariana Chiuffo and Guillermo Amico contributed to the experimental design, Gabriel A. Guerra and Bruno Alzugaray provided field work assistance. Parque Municipal Llao Llao provided the research permit. M. Sofia Campagna and Iván Barberá were beneficiary of a PhD scholarship of the National Scientific and Technical Research Council (CONICET) funded by the Argentinian government.

Funding

This study was funded by Ministerio de Ciencia, Tecnología e Innovación Productiva, Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación (Argentina), project PICT 2018-01566. M. S. Campagna and I. Barberá have a PhD scholarship from the National Scientific and Technical Research Council (CONICET-Argentina).

Competing Interests

The authors responsible of this study have no relevant financial or non-financial interests to disclose.

Authors Contributions

Campagna M. Sofía and Morán-López T. designed and performed the field experiments and wrote the original draft. Campagna M. Sofia, Barberá I., and Morán-López T. analyzed the data. Morales J.M provided experimental design and data analysis advise and made writing revisions. Barberá I. made writing revisions. Morán-López T. obtained the funding.

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Figures

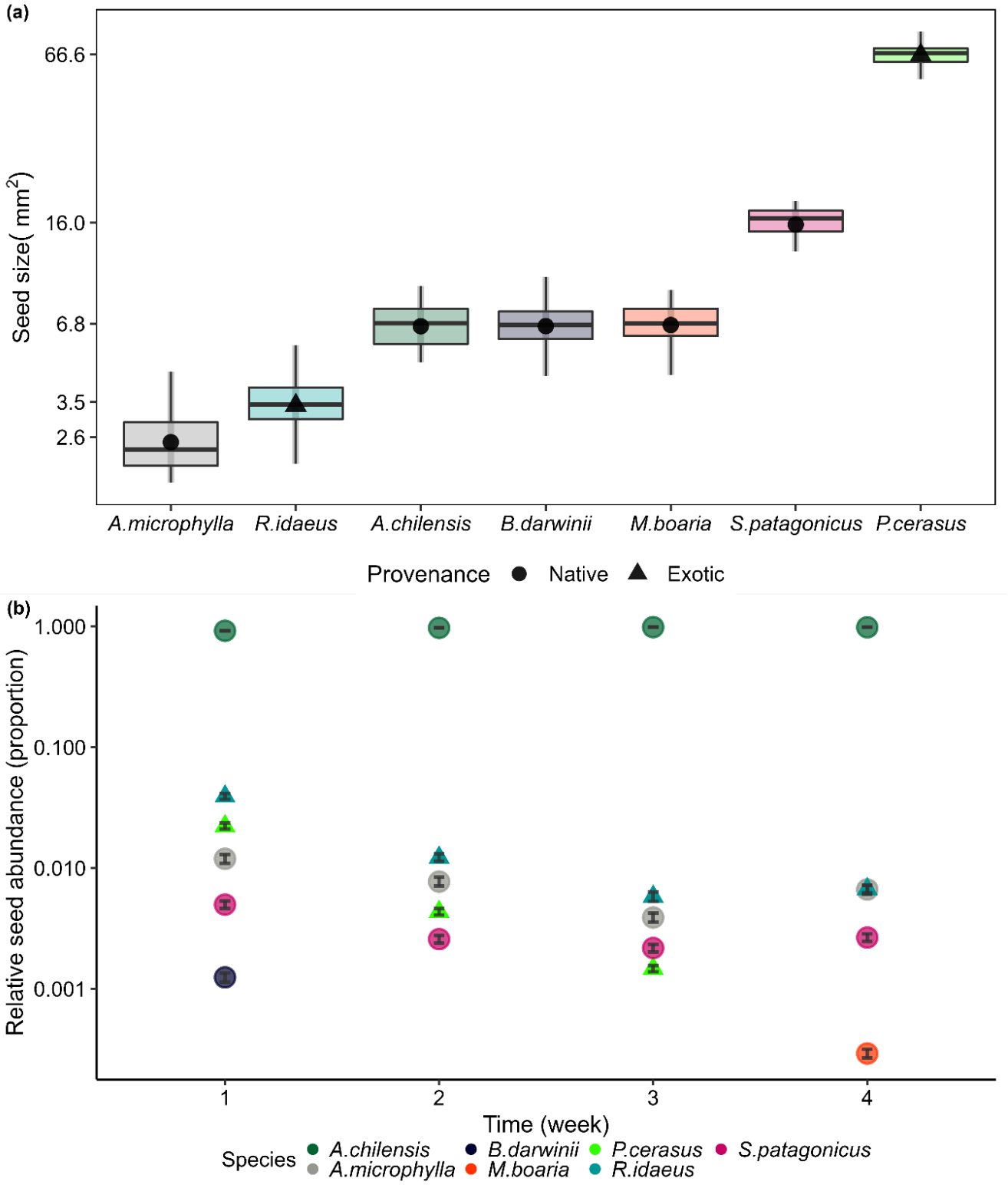

Figure 1

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. Native seeds are represented with circles, exotics wit triangles. Dots depict mean values of estimated relative abundances, whiskers 90% quantiles. In both panels note the logscale for Y-axis

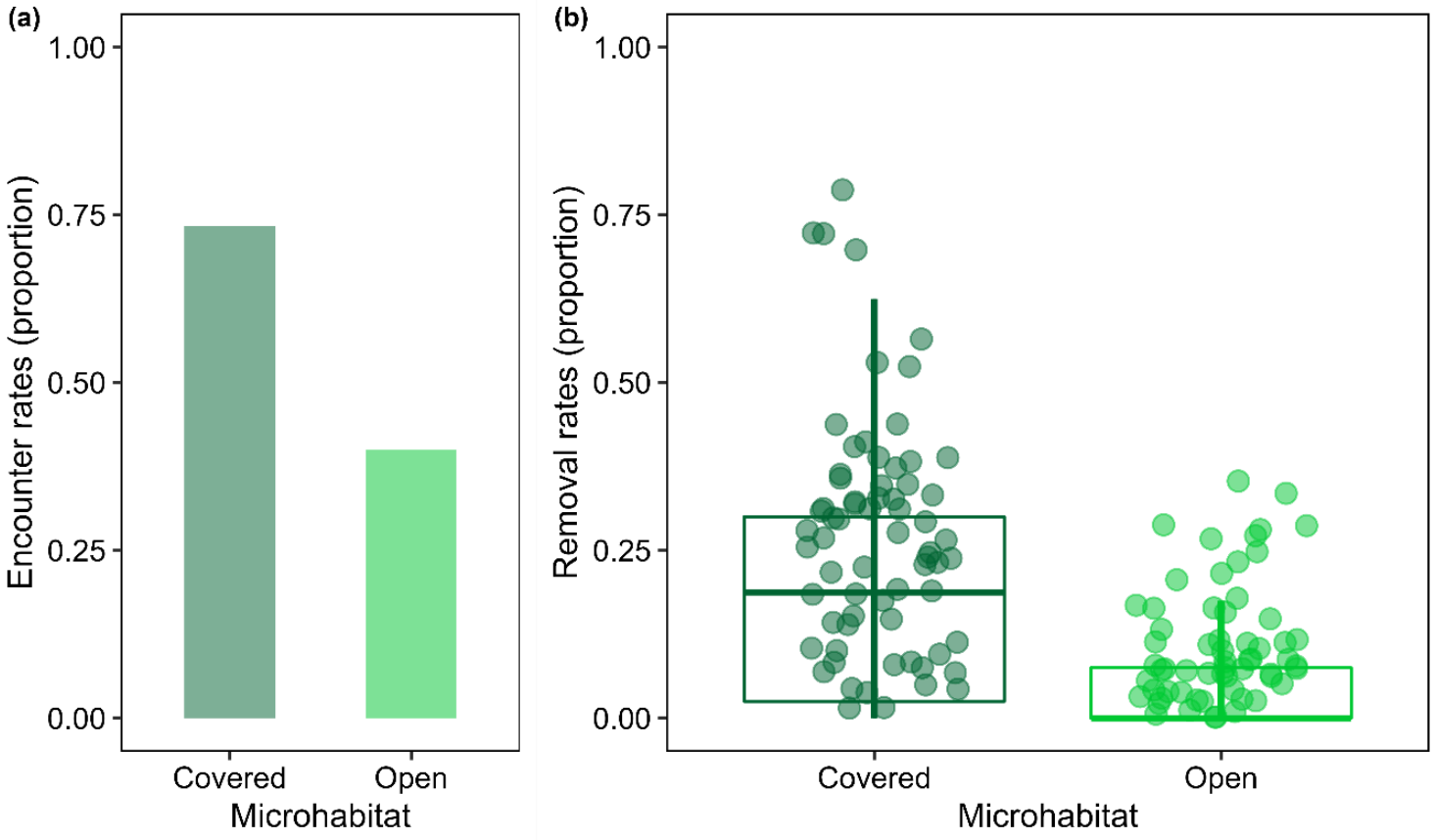

Figure 2

a Proportion of plots with seed removal after 24 h of seed offering and **b** seed removal rates after 72 h with respect to microhabitat (cover and open). In **b** dots represent removal rates per plot and week. Results of model fit can be found in Table 1

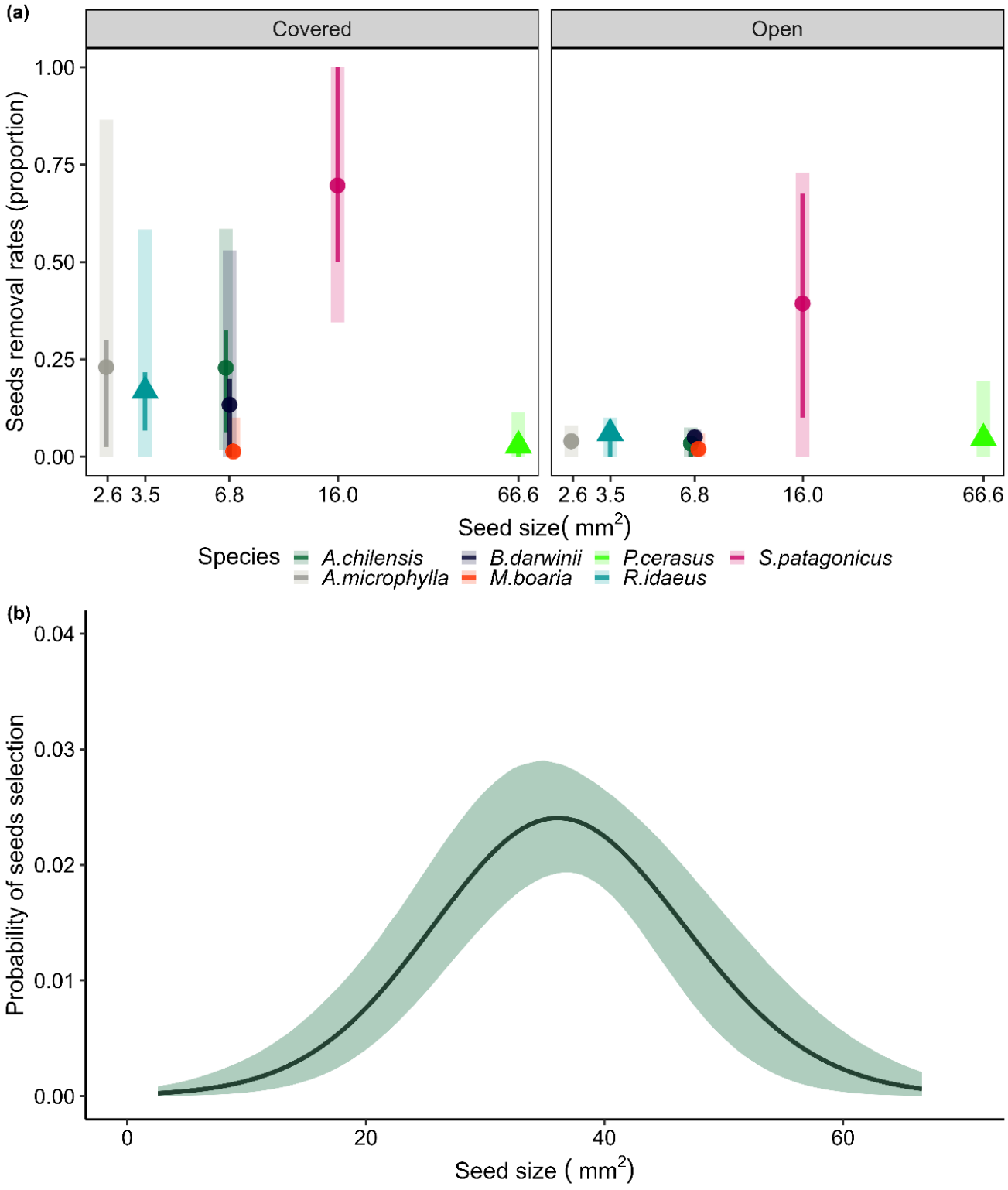

Figure 3

a Relationship between species seed removal rates and seed size. Dots represent mean removal rates of native and exotic species (circle and triangle, respectively) across plots and throughout the season. Dark and light lines depict the [0.25-0.75] and [0.05-0.95] quantiles. To improve data visualization X-axis was log-scaled. **b** Probability of seed selection by rodents as a function of size according to the

hypergeometric regression adjusted to data (Table 2). Line represents mean model predictions and ribbon 90% credible intervals

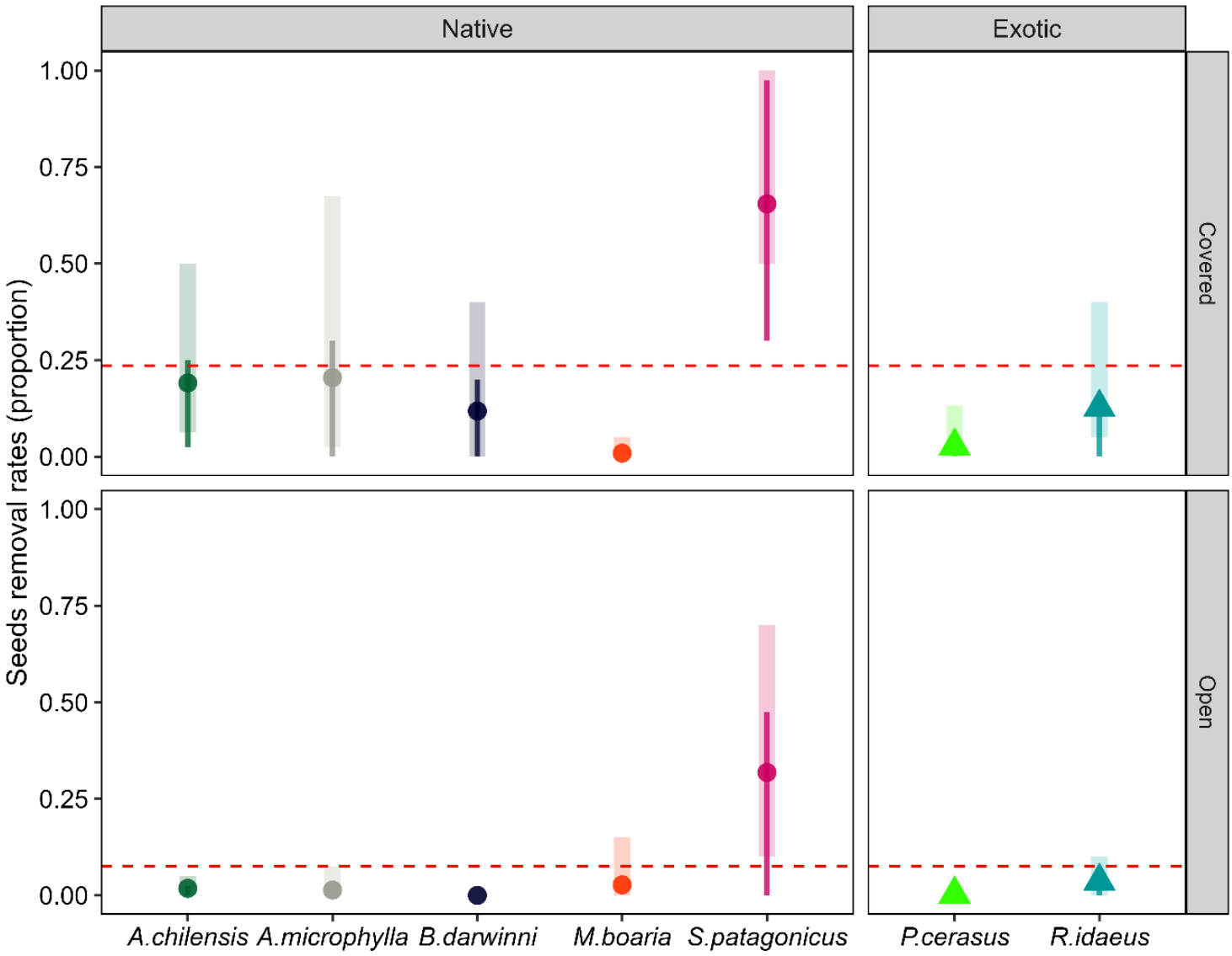

Figure 4

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

Supplementary Files

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