

Native and exotic species post - dispersal seed predation: a community scale approach

Maria Sofia Campagna (✉ sofiacampagna@hotmail.com)

INIBIOMA: Instituto de Investigaciones en Biodiversidad y Medioambiente <https://orcid.org/0000-0001-6752-5504>

Ivan Barberá

INIBIOMA: Instituto de Investigaciones en Biodiversidad y Medioambiente

Teresa Morán-López

INIBIOMA: Instituto de Investigaciones en Biodiversidad y Medioambiente

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Abstract

Seed predation is one of the most important biotic filters that determines whether an exotic species can become part of the community. Rodents are generalist seed consumers whose feeding preferences can affect the exotic species recruitment. Their foraging decisions are often modulated by seed traits, abundance, and the environmental context in which rodents encounter seeds. Besides, the consumption preference for exotic seeds may depend on how different they are from natives. We evaluated the combined effect of species-specific seed size, their relative abundance, and vegetation structure on predation rates of native and exotic plant species in a Patagonian forest, where two species of contrasting seed sizes are naturalized (*Prunus cerasus* and *Rubus idaeus*). We performed a cafeteria experiment in which we offered seeds of native and exotic species in paired plots located in microhabitats with shrub cover or open. In plots located under shrub cover seed predation rates were 2.3 times higher than in open areas. Feeding preferences of rodents were driven by seed size, selecting seeds of intermediate sizes. As result, they strongly avoided large exotic *Prunus* seeds, but consumed intermediate *Rubus* seeds at similar rates to natives. Thereby, in our system, size is a strong modulator of post-dispersal predation of exotic seeds and rarity does not confer any advantage to exotics. Low predation rates in open areas suggest that they could be regeneration foci for all species. Future work quantifying recruitment across microhabitats will allow to evaluate if patterns here found have an imprint in the seedling 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 capability of exotic species to become part of the recipient community. If generalist granivores preferentially consume exotic seeds, they will impose a biotic barrier to the invasion process (Maron et al. 2012; Nuñez, Simberloff, and Relva 2008; Pearson et al. 2014). In contrast, if exotic seeds are systematically avoided, they will have a recruitment advantage over natives (Connolly et al. 2014; Lucero and Callaway 2018; Pearson, Callaway, and Maron 2011). Therefore, understanding the feeding preferences of generalist granivores will improve our predictions about the potential of exotic species to invade new areas (Larios et al. 2017).

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 harness, nutrient content, phenolic compounds (Blate et al. 1998; Gong, Tang, and Wang 2015; Sidhu and Datta 2015), seed size has been pointed out as the most important modulator of their eating preferences (Dylewski et al. 2020). In general, seed size effects are not unequivocal but depend on the range of seed sizes present in the community (e.g., positive effects of size in small-seeded grasslands, while negative in

large-seeded forests (Radtke 2011). Such context-dependency may explain the contrasting results found in the literature with respect to the role of rodents in biological invasions, with large exotic seeds having high consumption rates (Nuñez, Simberloff, and Relva 2008) as well as escaping predation (Pearson, Callaway, and Maron 2011). It is expected that exotic seed with contrasting characteristics to those of natives will be perceived as a novel food item and they will have differential consumption rates (Pearson et al. 2014; Pearson et al. 2018; Pearson, Callaway, and Maron 2011). Also, whether exotic seeds are over or under-predated by granivorous, will depend on the sign of seed size effects in the community and the size of exotic seeds 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 a higher probability of rodents to encounter and be attracted to areas with abundant seeds (e.g. Baraibar et al. 2012; Batisteli et al. 2020; Myster 2003; Wang 2020). In contrast, the effects of species relative abundance at landscape and community scales have been largely overlooked in spite that it can affect recruitment success at early stages of the invasion process. Before exotic species become invasive, their propagule pressure tends to be low relative to natives (Křivánek, Pyšek, and Jarošík 2006; Pyšek et al. 2015; Simberloff 2009), and hence, preferential consumption of abundant seeds may facilitate exotic species overpassing the post-dispersal predation barrier. Therefore, evaluating density-dependent seed predation at landscape scales will provide new insights about the potential advantages of being rare at initial stages of the invasion process.

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). Lack of antipredatory 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). In addition, to avoid exposure to predators, rodents may reduce the time devoted to seed selection in open areas (Morán-López et al. 2018) becoming opportunistic foragers (Perea et al. 2011). Consequently, the probability of predation may not depend on seed traits, equalizing seed consumption rates across species. In the context of biological invasions, such shifts in rodent activity and behavior may turn open areas into invasion foci, where exotic species have a higher probability of escaping predation and recruiting (Pearson et al. 2014).

In this work, we estimated the combined effect of species-specific seed size, landscape-scale relative abundances, and shrub cover on predation rates of native and non-native species in a Patagonian temperate forest. In our study area, two species with contrasting seed sizes, *Rubus idaeus* and *Prunus cerasus*, have established a self-sustained population (i.e., naturalized). 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 relatively rare in the community, though during the fruiting season *Rubus* seeds are 1.5 times more abundant than those of *Prunus* (1.63% vs 0.93%). Finally, tree

falls create forest gaps where the availability of antipredatory cover is low (García, Zamora, and Amico 2011). We expected a positive effect of seed size on predation rates given that seeds of the recipient community are small (< 5 mg) (Online Resource 1) (Dylewski et al. 2020). Consequently, rodents may preferentially consume large *Prunus cerasus* seeds, whereas *Rubus idaeus* seeds will be consumed at similar rates to natives. In addition, we expected rarity to confer an advantage to exotic species, since a positive density-dependent response to seed abundance has been previously observed in the area (García, Zamora, and Amico 2011). Finally, we expected that the biotic filter of seed predation will be attenuated in areas of low shrub cover due to decreased rodent activity and a less selective foraging (Germain et al. 2013).

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 tree 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 *Abrothrix olivacea* (approximately 25 gr., *Cricetidae* family) (Caccia, Chaneton, and Kitzberger 2006; Nuñez, Simberloff, and Relva 2008).

Landscape-level Seed Abundance

We estimated the landscape-level seed availability using species-specific bootstrap samples of seed production species 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, we monitored the number of fruits present (in branches and in the canopy) and calculated the proportion of fruits missing in the branches (due to dispersal by birds or natural fall due to ripening). This informed about the number of

fruits whose seeds were present in the soil and had become 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 Online Resource 2 for further details.

Cafeteria Experiment

To assess the combined effect of species-specific seed size, weekly relative abundance and vegetation structure on post-dispersal seed predation 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 a pair of plots, one located under shrub cover (> 50% of cover in a buffer of 10 m around the plot) and another without shrub cover (open areas, hereafter). 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 (Online Resource 2). 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). Seeds were glued with nontoxic odorless adhesive and manipulated with gloves to avoid human odor (Moyano et al. 2019). We monitored seed consumption after 24 h, 72 h, and one week after seeds offering. The species-specific seed size was calculated as the seed area (mm^2). We measured the major and minor seed diameter in 50 seeds per species with a gauge, and then we estimated the area assuming oval or spherical shapes (Online Resource 1).

Statistical analysis

Effects of shrub cover on plot encounter and seed predation

To estimate the degree of rodent activity in the study area, we evaluated the effect of 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 predation in the first 24 hours after

offering (1 = at least one seed of any species was predated; 0 = no seed predation; Online Resource 3). We included shrub cover as a categorical predictor (under cover vs. open) and site as a random factor in the intercept to account for site-specific spatial variability in rodent activity.

Besides plot encounter, rodents may prefer to predate more intensively in microhabitats with shrub cover, where exposure to predators is reduced. Consequently, to test the effect of shrub cover on overall predation rates, we performed a Generalized Linear Mixed Model (GLMM) with a binomial response (logit link) (Online Resource 3). We modeled the proportion of seeds consumed in each plot as a function of the shrub cover and the site was included as a random effect 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 ($R_{hat} < 1.01$) and sufficient effective sample sizes ($n_{eff} > 2500$), we assessed model fit by means of posterior predictive checks (Online Resource 3). See Online Resource 3 for full models 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 shrub cover of seed offering plots (under cover vs. open). We assumed that the number of seeds consumed by each species, each week, and in each plot followed a (multivariate) Wallenius' hypergeometric distribution (Fog 2008), which considers the number and identity of seeds available in each foraging event. 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 (seeds were not replaced after predation). We modelled the seed selection probability (multinomial logit link function) as a function of the species-specific seed size (with a quadratic effect to account for hump-shaped responses, Dylewski et al. 2020), their relative abundance in the landscape, and the interaction of both covariates with shrub cover (Online Resource 3). 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 abundance were log-transformed and standardized before analyses. 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 ($R_{hat} < 1.01$) and effective sample sizes ($n_{eff} > 9000$), we assessed model fit by means of posterior predictive checks (Online Resource 3). From posterior distributions we calculated mean effects and credible intervals (q0.025, q0.975). For specifications of priors, model structure and distributions see Online Resource 3.

All analyses and figures were performed in R version 4.0.4 (R Core Team 2021).

Results

As expected, the probability of seed encounter 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. 2). Similarly, predation rates were almost 4 times higher in plots under shrub cover (19% and 5%, covered and open respectively).

Regarding seed selection by granivores, we observed a hump-shaped response with respect to seed size (Fig. 3), with a positive effect that reversed for seeds larger than 20 mm² (as indicated by the negative effect of the quadratic term, Table 2). Contrary to our expectations, we found no effect of the relative abundance of seeds at landscape scale, and the presence of shrub cover did not affect the foraging decisions of granivores (non-significant interaction terms of cover with seed size or relative abundance, Table 2). When comparing exotic species with natives, predation rates of *Rubus idaeus* were comparable to those of native species, whereas seeds of *Prunus cerasus* were under-predated (Fig. 4). In fact, predation rates of *Prunus* drove the hump-shaped response of predation rates to seed size (Fig. 3a).

Discussion

The selective foraging of granivores can result in differential probability of species recruitment based on their traits and abundances (Germain et al. 2013; Larios et al. 2017; Lichti, Steele, and Swihart 2017). We found a hump-shaped relationship between predation rates and seed size (Fig. 3), which suggests that rodents preferred intermediate-sized seeds, a pattern consistent with previous studies in temperate forests (Dylewski et al. 2020). Large seed size variability in temperate forests, with small and large-seeded species, has been suggested as the underlying cause of such hump-shaped responses. However, our native community is characterized by small seeded species (< 5 mg) (Dylewski et al. 2020). Accordingly, when considering only native plants, rodents preferred large seeds. In fact, the negative effects of seed size were mainly driven by low predation rates on *Prunus cerasus*. 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 natives species (Blate et al. 1998). Irrespectively of the seed trait, our results support the idea that when an exotic species enters 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 than those of natives (e.g., Connolly et al. 2014; Pearson et al. 2011).

Contrary to our predictions, we found that seed predation by rodents was not mediated by species-specific relative abundance at the landscape scale. This was unexpected, since density-dependent effects have been frequently found at local scales (Baraibar et al. 2012; Daedlow et al. 2014; Myster 2003; Pardini, Patten, and Knight 2017) and foraging on abundant resources is usually advantageous as it decreases searching times (Hulme 1993; Cabin et al. 2000; Baraibar et al. 2012). This lack of response may be due to the spatial scale at which we measured the relative abundance of seeds. It is possible that rodents are more sensitive to the relative abundance at spatial scales matching their home ranges, where they usually search for food (< 0.5 ha vs. 2.4 ha of our study area (Monteverde and Hodara 2017; Valladares-gómez et al. 2020)). Thus, rodent foraging decisions would be driven by the relative abundance of species at smaller spatial scales (e.g., neighborhoods) (Baraibar et al. 2012; Garzon-Lopez et al. 2015; Ostoja et al. 2013). Hence, predation rates of exotic seeds would depend on their spatial arrangement (i.e., patchy distribution) rather than on community composition. Also, in our study system rodents could be selecting species with a certain set of traits (i.e., *Schinus patagonicus* seeds), Fig. 4) irrespectively of their relative abundance (see (Veech 2001) for similar results). Independently of the underlying mechanisms, our results indicate that in our system rarity in the recipient community does not confer an advantage to exotic species during the post-dispersal seed predation filter. As expected, post-dispersal seed predation was modulated by the vegetation structure (Fig. 2). Predation rates in open microhabitats were much 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). In general, rodents concentrate their activities under shrub cover, which offers antipredatory shelter, increasing the probability of encountering and consuming seeds (Kollmann and Buschor 2003; Schnurr et al. 2004). We expected a more opportunistic foraging by rodents in open microhabitats in response to decreased handling times to avoid exposure to predators (Perea et al. 2011). However, rodent selectivity did not vary with vegetation cover, suggesting that perceived predation risks in open areas were moderate (Table 2). Taken together, our results suggest that open microhabitats could act as regeneration foci. Thus, seeds of all species, including exotics, had a higher probability to survive in open areas, at least in the short-term (Fig. 4). This interpretation should, however, be carefully considered because cafeteria experiments inform about patterns of activity and feeding preferences of seed predators but cannot draw strong conclusions about the final seed fate. Seeds that are not initially selected can be predated over longer periods of time, blurring short-term patterns. To test whether increased short-term seed survival affects recruitment, we are currently monitoring seedling communities in open and covered microhabitats.

Overall, our work shows that in our area the probability of seed predation is mediated by species-specific seed size and vegetation structure. In particular, *Prunus cerasus* seeds, which were 4 times larger than the largest natives, were systematically avoided. Besides, in open microhabitats, seeds had an average probability of surviving predation 2.3 times higher than under cover (Fig. 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 modulator of their ability to overpass the post-dispersal predation filter (Dylewski et al. 2020; Radtke 2011). Also, our results suggest that in Patagonian temperate forests, open microhabitats can act as regeneration foci for all species,

including exotics. Future work comparing seedling density and composition across microhabitats will provide insights about the imprint of rodent activity and feeding preferences on the composition of the community of recruits.

Declarations

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Conflicts of interest/Competing interests

The authors declare that they have no conflict of interest.

Ethics approval

Not applicable

Consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and material

The datasets analyzed during the current study is available from the corresponding author on reasonable request.

Code availability

The code made and used in the current study is available from the corresponding author on reasonable request

Author Contributions

MSC and TML designed and performed the field experiments and wrote the original draft. MSC, IB, and TML analyzed the data. JMM provided experimental design and data analysis advice and made writing revisions. IB made writing revisions. TML obtained the funding.

References

1. 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
2. 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. doi: 10.1111/aec.12922
3. 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. doi: 10.2307/35463 73
4. Brewer S (2001) Predation and dispersal of large and small seeds of a tropical palm. *Oikos* 92(2): 245-255
5. Boone SR, Mortelliti A (2019) Small mammal tree seed selection in mixed forests of the Eastern United States. *For Ecol Manage* 449:117487. doi: 10.1016/J.FORECO.2019.117487
6. Bürkner P (2017) brms: An R Package for Bayesian Multilevel Models Using Stan. *J Stat Softw* 80:1–28. doi.org/10.18637/jss.v080.i01
7. Cabin RJ, Marshall DL & Mitchell RJ (2000) The demographic role of soil seed banks. II. Investigations of the fate of experimental seeds of the desert mustard *Lesquerella fendleri*. *The Journal of Ecology* 88, 293–302.
8. Cabrera AL (1971) Sociedad Argentina de Botánica. *Boletín de la Sociedad Argentina Botánica* XIV:1–50
9. Caccia FD, Chaneton EJ, Kitzberger T (2006) Trophic and non-trophic pathways mediate apparent competition through post-dispersal seed predation in a Patagonian mixed forest. *Oikos* 113:469–480. doi: 10.1111/j.2006.0030-1299.14390.x
10. 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. doi: 10.1890/15-2147.1. PMID: 27859154.
11. Connolly BM, Pearson D, Mack RN (2014) Granivory of invasive, naturalized, and native plants in communities differentially susceptible to invasion. *Ecology* 95:1759–1769
12. Crawley MJ (2000) Seed predators and plant population dynamics. In: Fenner M (ed) *Seeds: the ecology of regeneration in plant communities*. Cabi Wallingford UK, United States, pp 167–182
13. Daedlow D, R. WP, B. B, et al (2014) Weed seed predation rate in cereals as a function of seed density and patch size, under high predation pressure by rodents. *Weed Res* 54:186–195
14. 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>

15. Fog A (2008) Sampling Methods for Wallenius' and Fisher's Noncentral Hypergeometric Distributions. *Communications in Statistics, Simulation and Computation*. Vol. 37, no. 2, pp 241-257.
16. Fog A (2022) Biased Urn Theory. <https://cran.r-project.org/web/packages/BiasedUrn/vignettes/UrnTheory.pdf>
17. 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>
18. Garzon-Lopez CX, Ballesteros-Mejia L, Ordoñez A, et al (2015) Indirect interactions among tropical tree species through shared rodent seed predators: a novel mechanism of tree species coexistence. *Ecol Lett* 18:752–760
19. 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>
20. Geyer CJ (2022) Package "mcmc". <https://cran.r-project.org/web/packages/mcmc/mcmc.pdf>
21. 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>
22. Hulme PE (1993) Post-dispersal seed predation by small mammals. *Symposium of the Zoological Society of London*, 65, 269–287.
23. Hulme PE (1994) Post-dispersal seed predation in grassland: its magnitude and sources of variation. *J Ecol* 82:645–652.
24. Hummer KE and Peacock DN (1994) Seed dimension and weight of selected *Rubus* species. *HortScience* 29(9): 1034-1036.
25. Kollmann J, Buschor M (2003) Edges effects on seed predation by rodents in deciduous forests of northern Switzerland. *Plant Ecol* 164:249–261
26. Křivánek M, Pyšek P, Jarošík V (2006) Planting History and Propagule Pressure as Predictors of Invasion by Woody Species in a. *Conserv Biol* 20:1487–1498. <https://doi.org/10.1111/j.1523-1739.2006.00477.x>
27. Larios E, Búrquez A, Valenzuela G, et al (2017) Post-dispersal seed predation in relation to selection on seed size in *Dithyrea californica*. *Evol Ecol Res* 18:651–662
28. Larios L, Pearson DE, Maron JL (2017) Incorporating the effects of generalist seed predators into plant community theory. *Funct Ecol* 31:1856–1867. <https://doi.org/10.1111/1365-2435.12905>
29. 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>

30. 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>
31. Lucero JE, Callaway RM (2018) Native granivores reduce the establishment of native grasses but not invasive *Bromus tectorum*. *Biol Invasions* 20:3491–3497
32. Maron JL, Pearson DE, Potter T, Ortega YK (2012) Seed size and provenance mediate the joint effects of disturbance and seed predation on community assembly. *J Ecol* 100:1492–1500. <https://doi.org/10.1111/j.1365-2745.2012.02027.x>
33. 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
34. 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
35. Morán-López T, Carlo TA, Amico G, Morales JM (2018) Diet complementation as a frequency-dependent mechanism conferring advantages to rare plants via dispersal. *Funct Ecol*. <https://doi.org/10.1111/1365-2435.13152>
36. Mortelliti A, Ilona PG, Shawn F, et al (2019) Small mammal controls on the climate-driven range shift of woody plant species. *Oikos* 1–13. <https://doi.org/10.1111/oik.06643>
37. 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>
38. Muñoz A and Bonal R (2008) Are you strong enough to carry that seed? Seed size/body size ratios influence seed choices by rodents. *Animal Behaviour* 76(3):709-715.
39. Muñoz E and Garay A (1985) Caracterización climática de la provincia de Río Negro. INTA- EERA. S.C. de Bariloche. Informe técnico n° 56.
40. 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
41. Muschetto E, Mazia N, Cueto GR, Busch M (2015) Are rodents a source of biotic resistance to tree invasion in P ampean grasslands? Tree seed consumption under different conditions. *Austral Ecol* 40:255–266
42. 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>
43. 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>
44. Ostoja SM, Schupp EW, Durham S, Klinger R (2013) Seed harvesting is influenced by associational effects in mixed seed neighbourhoods, not just by seed density. *Funct Ecol* 27:775–785
45. Pardini EA, Patten M V, Knight TM (2017) Effects of seed density and proximity to refuge habitat on seed predation rates for a rare and a common *Lupinus* species. *Am J Bot* 104:389–398

46. 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>
47. 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>
48. 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>
49. 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
50. 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
51. Radtke TM (2011) Granivore seed-size preferences. *Seed Sci Res* 21:81–83
52. R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
53. Sala OE et al. (2000) Global Biodiversity Scenarios for the Year 2100. 287:1770-1774 <https://doi.org/10.1126/science.287.5459.1770>
54. Schnurr JL, Canham CD, Ostfeld RS, Inouye RS (2004) Neighborhood analyses of small-mammal dynamics: impacts on seed predation and seedling establishment. *Ecology* 85:741–755
55. 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
56. 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>
57. Simberloff D, Martin JL, Genovesi P, et al (2013) Impacts of biological invasions: What's what and the way forward. *Trends Ecol. Evol.*
58. Thompson DB, Brown JH, Spencer WD (1991) Indirect facilitation of granivorous birds by desert rodents: experimental evidence from foraging patterns. *Ecology* 72:852–863
59. Valladares-gómez A 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
60. Veech JA (2001) The foraging behavior of granivorous rodents and short-term apparent competition among seeds. *Behav Ecol* 12:467–474
61. Wang B (2020) Seed density affects post-dispersal seed predation: evidence from a seed removal experiment of 62 species. 135–143. <https://doi.org/10.1111/1749-4877.12421>
62. Weiher E et al. (1998) Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* 81:309–322. <https://doi.org/https://doi.org/10.2307/3547051>.
63. Yarılgac T et al. (2005) Indigenous Sour Cherry (*Prunus cerasus* L.) Germplasm of Lake Van Basin. *Asian Journal of Plant Sciences*, 4: 558-561

Tables

Table 1. Summary of models testing the effect of shrub cover on seed predation rates. Probability of plot encountering during the first 24 hours after seeds offering (Bernoulli regression) and seed predation rates after 72 h (Binomial regression). The site where the seed-offering plot was located was introduced as a random effect in the intercept to account for site-specific spatial variability in rodent activity. Mean posterior distribution (mean effect), credible interval, 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 $f \geq 0.95$.

	Parameter	Mean	95 % CI	f	$\hat{R}$	n.eff
Probability of encounter						
Intercept (Shrub cover)	β_0	1.27	-0.03; 2.92	0.96	1.00	3548
Shrub cover (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
Predation rates						
Intercept (Shrub cover)	β_0	-1.49	-1.91; -1.11	1	1.00	2669
Shrub cover (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

Table 2. Summary of the seed selection model (factors driving foraging decision by granivores). Effects of species-specific size of seeds, their relative abundance, and the shrub cover (under cover as the reference category). Mean posterior distribution (mean effect), credible interval, 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 $f \geq 0.95$.

	Parameter	Mean	95% CI	f	$\hat{R}$	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 × Shrub cover (Open)	β_4	0.44	-0.70, 1.59	0.73	0.99	14884
Seed size ² × Shrub cover (Open)	β_5	-0.59	-1.86, 0.55	0.70	0.99	14507
Abundance × Shrub cover (Open)	β_6	0.01	-1.64, 1.63	0.50	1.00	9856

Figures

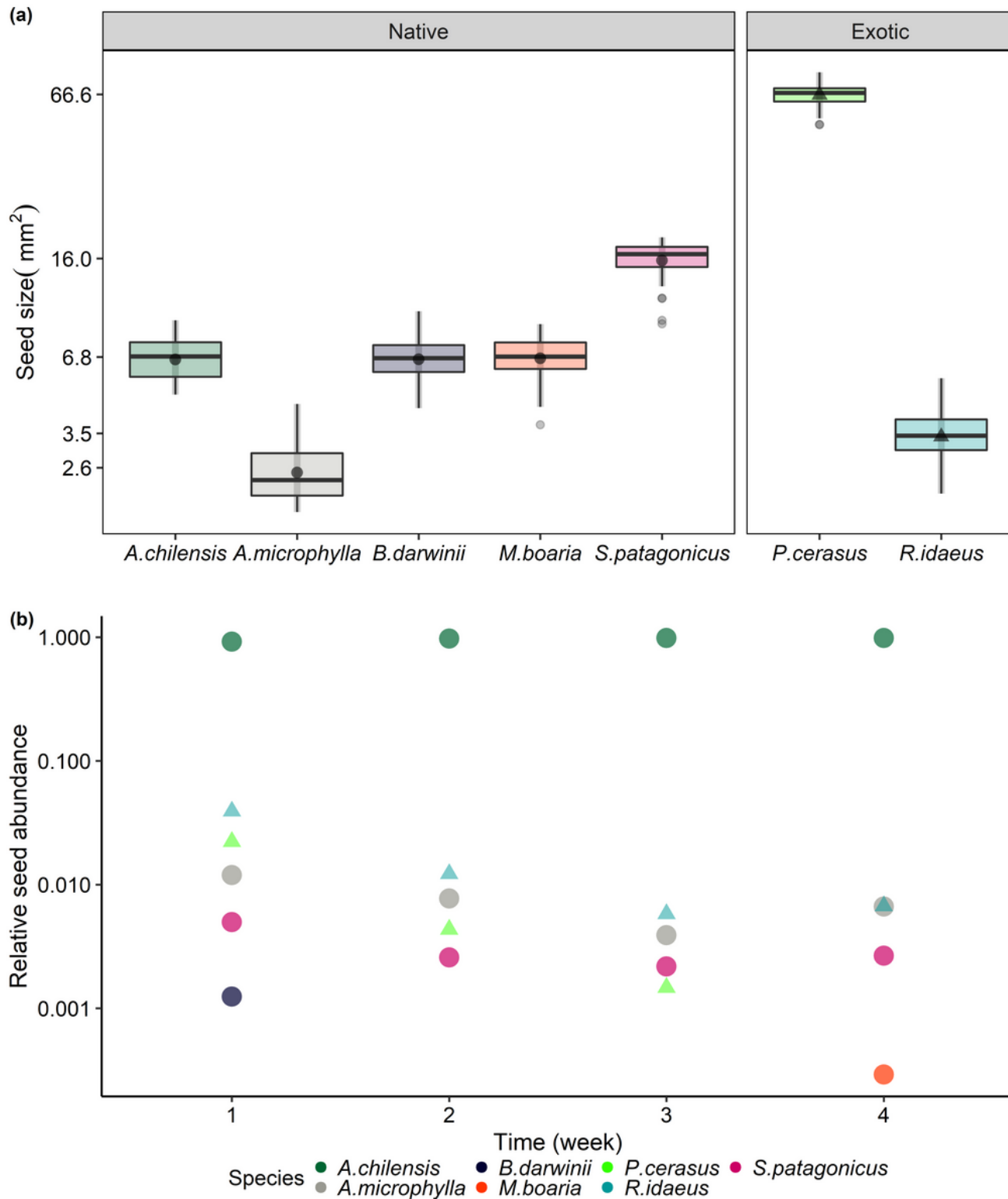


Figure 1

a Seed size of the native (closed circle, left) and exotic (closed triangle, right) fleshy fruit tree species present in the studied community (temperate Patagonian forest). Dots show the means (50 seeds per species); the box represents 50% of the data, the horizontal line indicates the median, lower and upper hinges correspond to the first and third quartiles (the 25th and 75th percentiles), and the lower and upper whiskers extend from the hinge to the largest or lowest value no further than $1.5 \times \text{IQR}$ (inter-quartile

range). **b** Species-specific relative abundance of native (closed circle) and exotic (closed triangle) seeds throughout the weeks in which we conducted the cafeteria experiment. Dots depict mean values across 2000 bootstrap samples to estimate relative seed abundance at landscape scale. Note the logscale for both Y axes

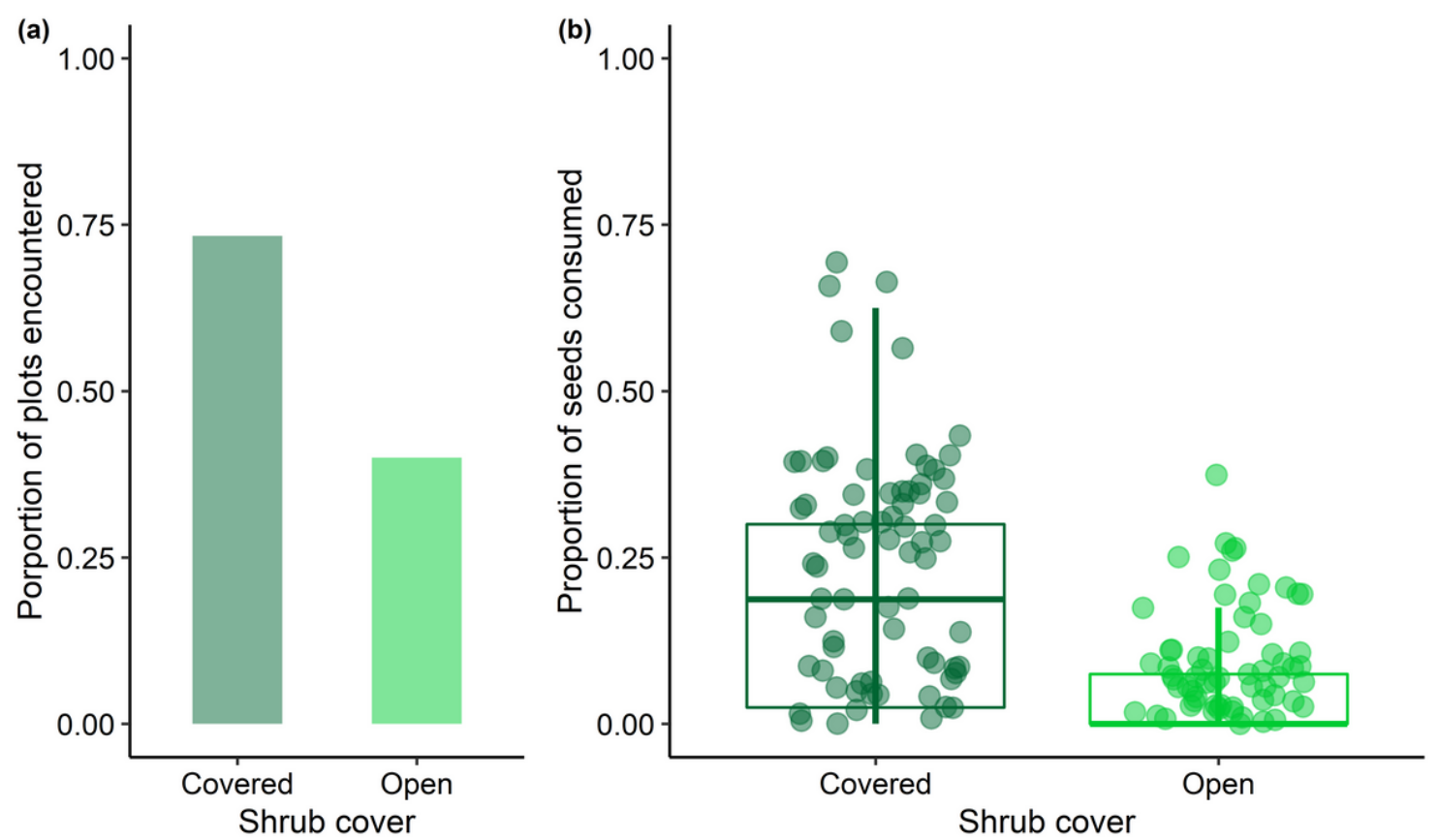


Figure 2

a Proportion of plots with seed predation after 24 h of seed offering and **b** proportion of seeds consumed after 72 h in plots located under shrub cover vs open microhabitats. In **b** dots represent consumption rates per plot and week (boxplot description in Fig. 1 legend)

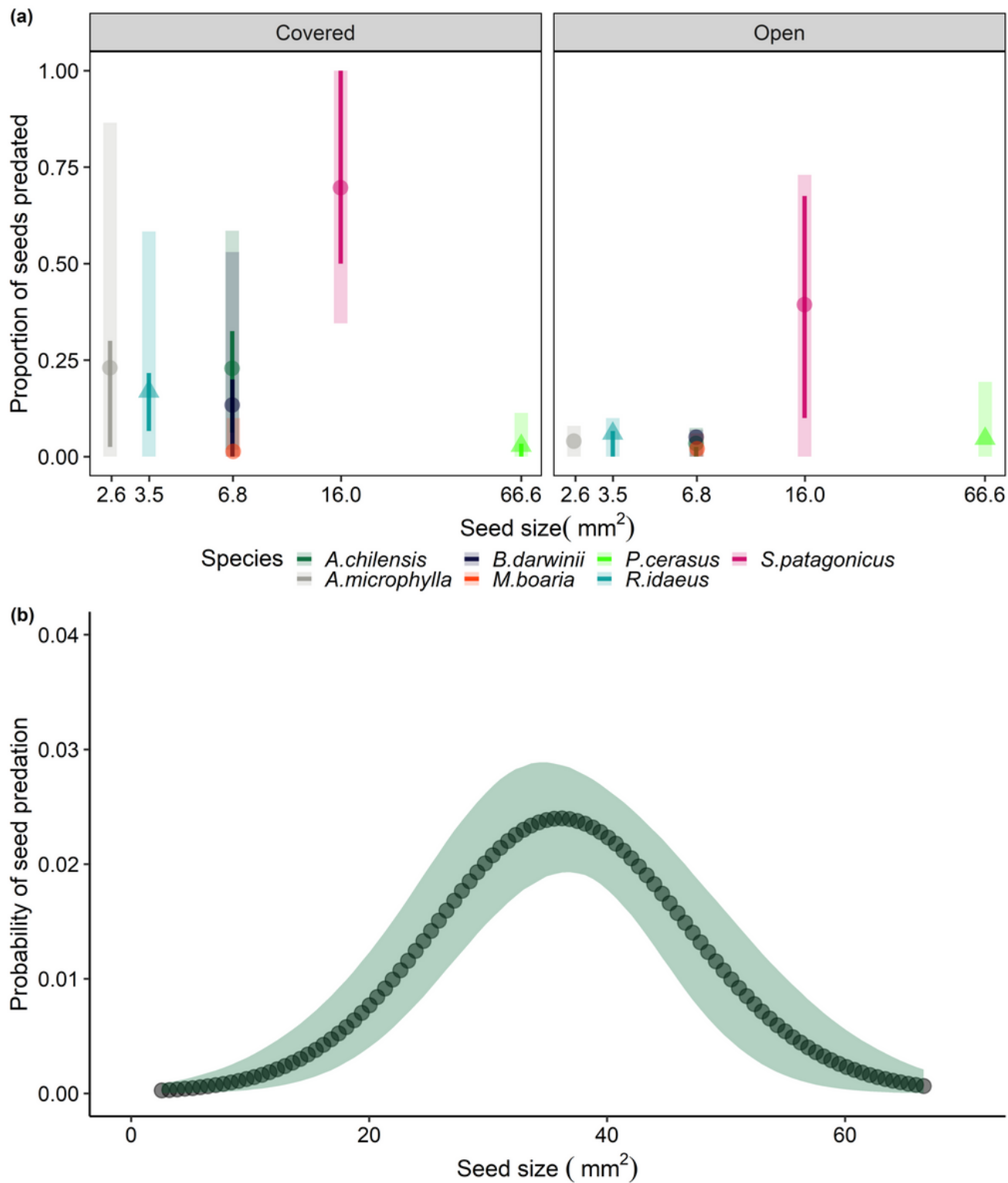


Figure 3

a Seed size effect on species-specific predation rates (proportion of seeds predated). Dots represent mean predation rates of native (closed circle) and exotic (closed triangle) species, across plots, throughout the season and dark and light lines depict the [0.25-0.75] and [0.05-0.95] observed percentiles in the data, respectively. Note the log scale for Y axis. **b** Predicted seed predation probability as a function of seed size. Each point represents a hypothetical species, and predation probabilities are the likelihood

of a predator choosing a seed if only one seed by species were offered. The ribbon represents the 90% credible interval of model predictions.

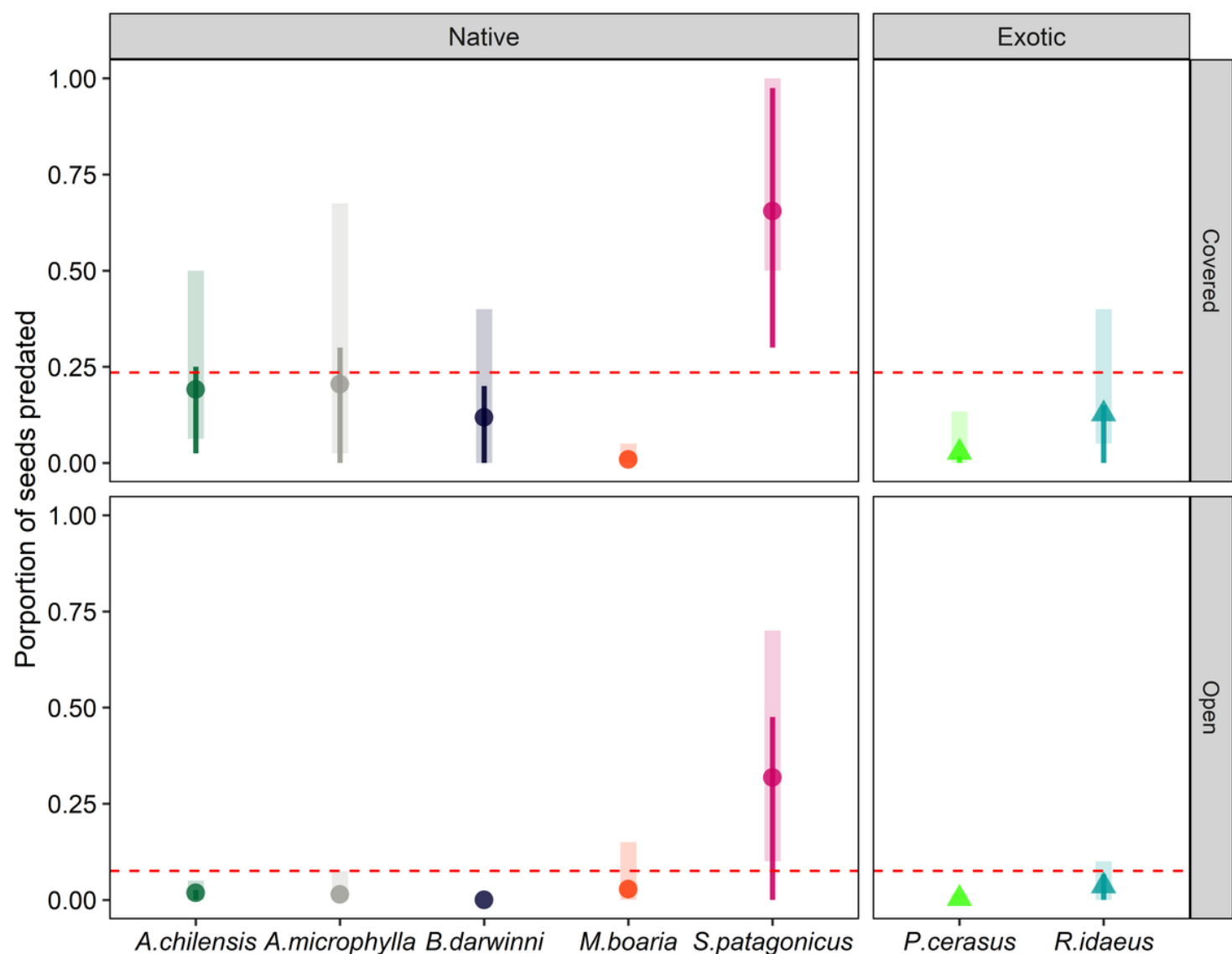


Figure 4

Seed predation rates by species throughout the 4 weeks of the cafeteria experiment. Native (closed circle, left) and exotic (closed triangle, right) species in plots located under shrub cover (upper) vs open microhabitats (lower). Dots represent mean values (across plots throughout the season), the dark and the light lines are the [0.25-0.75] and [0.05-0.95] percentiles of the data, respectively. The red line represents the mean predation rates of native species

Supplementary Files

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