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Post-dispersal seed predation in Patagonia temperate forest depends on habitat patchiness and seed species

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Abstract Post-dispersal seed predation is a key process regulating plant population dynamics and community composition. Because food preference (i.e., seed species selection) can interact with habitat features such as vegetation characteristics, integrating both is important for a better understanding of the processes that drive plant community structure. In order to study how forest habitat patchiness and seed species influence post-dispersal seed predation, we monitored seed predation of native common understory plant species in Patagonia temperate forests. By performing a cafeteria-style experiment, we assessed consumption on the three most common understory seed species, in forest interior and forest gaps. We found that seed predation by rodents differed between habitats and, independently, between seed species. Seed predation was more than 2 × higher in forest gaps than in forest interior, and medium-sized seed species were the least preyed-upon. Although counterintuitive, given that granivores such as rodents usually prefer sheltered habitats to forage, these results highlight the importance of site-specific variables in plant-granivore interactions.

Keywords Rodent seed predators · Cafeteria experiment · Habitat features · Seed species

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Introduction

Post-dispersal seed predation is a key process regulating plant population dynamics and community composition (Hulme 1998; Bricker et al. 2010; Maron et al. 2012; Hegstad and Maron 2019). Seed predation can be highly variable and influenced by multiple factors including seed predator abundance and behavior (Orrock et al. 2010), habitat characteristics, and seed traits (Kollman and Buschor 2003; García and Chacoff 2007; Moyano et al. 2019; Dylewski et al. 2020). Theory posts that while foraging, rodents should avoid low-quality food patches in favor of high-quality ones (MacArthur and Pianka 1966) and seek for safe patches while avoiding risky ones (the "foraging dilemma," McArthur et al. 2014). On the one hand, habitats with complex structure can enhance rodents foraging activity by offering shelter from predators (Morris and Davidson 2000; Kollman and Buschor 2003). For example, habitat variables such as substrate and distance to nearest tree in Mediterranean forests (Fedriani 2005), and grass and shrub cover in temperate northern forests (Kollman and Buschor 2003) have better explained seed predation by rodents than seed phenotypic traits. In temperate forest ecosystems, understory cover and patchiness have shown to be relevant in driving seed predation patterns (Abe et al. 2001; Schnurr et al. 2004). On the other hand, seed traits such as mass (Jansen et al. 2004), size (Dylewski et al. 2020), and volume (Moyano et al. 2019) have explained rodents preference for seeds. Therefore, because food preference (i.e., seed selection) can interact with or overcome habitat features such as vegetation characteristics (Pons and Pausas 2007; Booman et al. 2009; García et al. 2011), integrating both is important for a better understanding of the processes that drive plant community structure (Larios et al. 2017).

Patchiness or forest cover variations are fundamental drivers of diversity and community dynamics in forest ecosystems (e.g., Jackson and Wong 1994; Schnurr et al. 2004; Heinemman et al. 2006; Ushio et al. 2010; Echeverria et al. 2014). Particularly, the regeneration and persistence of tree species in southern temperate forests can depend on forest-clearing dynamics (Veblen 1985; Bustamante & Armesto 1995; Pollmann 2003). Gutiérrez et al. (2004) found that small-scale disturbances (e.g., tree-fall originated gaps) increased the heterogeneity of the forest floor, producing microsites that favor the coexistence of plants with different regeneration modes. Also, in forest gaps, seeds previous to perturbation or seeds coming from adjacent patches are important for native vegetation to recover (Armesto et al. 2001; Parkes et al. 2003; Guidetti et al. 2016). In this context, it is known that forest cover variation can alter plant-animal interactions such as seed predation (Schnurr et al. 2004; Caccia et al. 2006; Royo and Carson 2008) which can vary among habitats in response to biotic effects (e.g., direct and indirect predator cues; Sivy et al. 2011) or environmental drivers (e.g., vegetation context, Booman et al. 2009; Pons and Pausas 2007; moonlight, Kotler et al. 2010). Therefore, it is reasonable to expect that habitat change alter seed predation patterns (Diaz et al. 1999; García and Chacoff 2007), which in turn can influence forest composition and regeneration (Schreiner et al. 2000; García et al. 2005; Caccia et al. 2006).

In order to understand how forest habitat patchiness (forest interior vs. gaps) and seed species influence post-dispersal seed predation, we monitored seed predation of native common understory plant species in Patagonia temperate forests, by assessing consumption on three different native seed species in forest interior and forest gaps. Understanding how forest habitat heterogeneity affects seed predation is fundamental to understand plant community dynamics in forest ecosystems.

Methods

Study area

Our study was conducted in Llao-Llao Reserve, a 1220 ha area within Nahuel Huapi National Park in Patagonia–Argentina (41° 03′ S, 71° 30′ W), in Autumn 2005. Regional climate is humid in autumn–winter and dry in spring–summer, with 9 °C average annual temperature and 1800 mm average annual precipitation (Cabrera 1976). The native forest vegetation belongs to the Subantarctic biogeographical region (Cabrera 1976), the dominant tree species being the evergreen southern beech (*Nothofagus*

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dombeyi) and cordilleran cypress (*Austrocedrus chilensis*) (Mermoz and Martín 1986). Llao-Llao Reserve has been protected since the 1960s, but it was previously logged in certain areas, and canopy gaps of variable size have been generated by tree falls, giving the forest a patchy distribution (Amico et al. 2008). These gaps present some of the common understory vegetation dominated by the native shrub (*Aristotelia chilensis*) and native bamboo (*Chusquea culeou*) (Mermoz and Martín 1986). The main post-dispersal seed predators in the area are Cricetidae rodents ($\sim$ 25 gr.) such as the long-haired grass mouse (*Abrothrix hirta)*, long-tailed mouse (*Oligoryzomys longicaudatus*), and olive grass mouse (*A. olivacea*) (Caccia et al. 2006; Nuñez et al. 2008; García et al. 2011). So far, there are no reports of scatter-hoarding rodents, and the authors found no evidence of bird seed predation (no removed soiled or bird excrements around seed depots). As the experiment was during Autumn, invertebrate or insect predation can be negligible.

Cafeteria experiment

In order to study if post-dispersal seed predation varied between forest interior and forest gaps (“habitat”) and if there was a preference for different seeds (“species”), we established a cafeteria-style experiment (Lobo et al. 2009; Pearson et al. 2014; Moyano et al. 2019). We selected six forest gap sites distributed haphazardly inside the Llao-Llao Reserve and six intact native forest interior sites, with gap and forest habitats differenced by the occurrence of tree canopy cover, forest having $> 80\%$ and gaps $< 10\%$ (see Fig. 1a for a schematic representation). As for seeds, we chose the three most common understory native species in these forests (García et al. 2011) and their seeds represent an optimal gradient of size/mass, from larger to smaller: *Schinus patagonicus* (18.81 $\text{mm}^{2\text{-}} \pm 0.21\text{mm}^2$; 0.607 g $\pm$ 0.019 g); *Maytenus boaria* (4.95 $\text{mm}^2 \pm 0.03$ mm^2; 0.368 g $\pm$ 0.029 g); and *Aristotelia chilensis* (3.25 $\text{mm}^2 \pm 0.02$ mm^2; 0.185 g $\pm$ 0.017 g) (Supplementary Material, Figure S1). These species are representative of the understory (as pioneers of clearing colonization), unaffected by masting behavior (enabling us to extrapolate to the medium-term) and endozoochorous (thus homogenizing the functional group and its implications in expected patterns of spatial distribution of deposition). Seeds were obtained from fruits randomly collected on plants at the study site, in order to estimate specific individual seed mass/size and to prepare a seed pool for experimental depots.

In the experiment, we offered seeds to predators in the field by attaching them to wooden popsicle sticks holding three seeds of each species (nine seeds total per stick, Fig. 1c). Seeds were fastened to the sticks in a random order, using non-toxic glue, wearing gloves to prevent human scent to impregnate them (García et al. 2011). At each forest and gap sites, we randomly placed seed depots (= set of three wooden popsicle sticks; Fig. 1b, c) at a minimum distance of 25 cm each, nailed to the ground with a wire staple over each stick center. Because understory cover is an important factor influencing seed predation rate (Caccia et al. 2009; Royo and Carson 2008), we placed seed depots under parental species shrubs. This also controls for possible differences in real seed rain densities, usually expected to be stronger under bush, than far from bush (especially in clearings; García et al. 2011). Initially, 10 seed depots were placed separated at least 30 m from each other, and sites were more than 200 m apart (Fig. 1b). We evaluated seed predation after 48 h of installing the experiment, a period comparable with previous studies in several environments (Hulme 1994; Kollman et al. 1998; Hulme & Borelli 1999; Orrock 2015). Both the seeds removed from the popsicle sticks and those damaged (with obvious bite marks) but remaining in place were considered as predated.

Statistical analyses

To determine if seed predation (response variable) differed between “habitats” (“forest interior,” “forest gaps”), we used generalized linear mixed models (GLMM) (Fig. 1). Seed predation was calculated as the proportion of predated seeds after 48 h. To evaluate if there was a preference for seed “species,” we included it as a predictive variable, with factors “Small” (*A. chilensis*), “Medium” (*M. boaria*), and “Large” (*S. patagonicus*). We also considered the interaction between factors, in order to test if potential differences between species depended on the habitat type. We assumed a binomial distribution, using a GLMM based on Laplace approximation and a logit link function (lme4 package, *glmer* function, Bates et al. 2015). Since our experimental design had

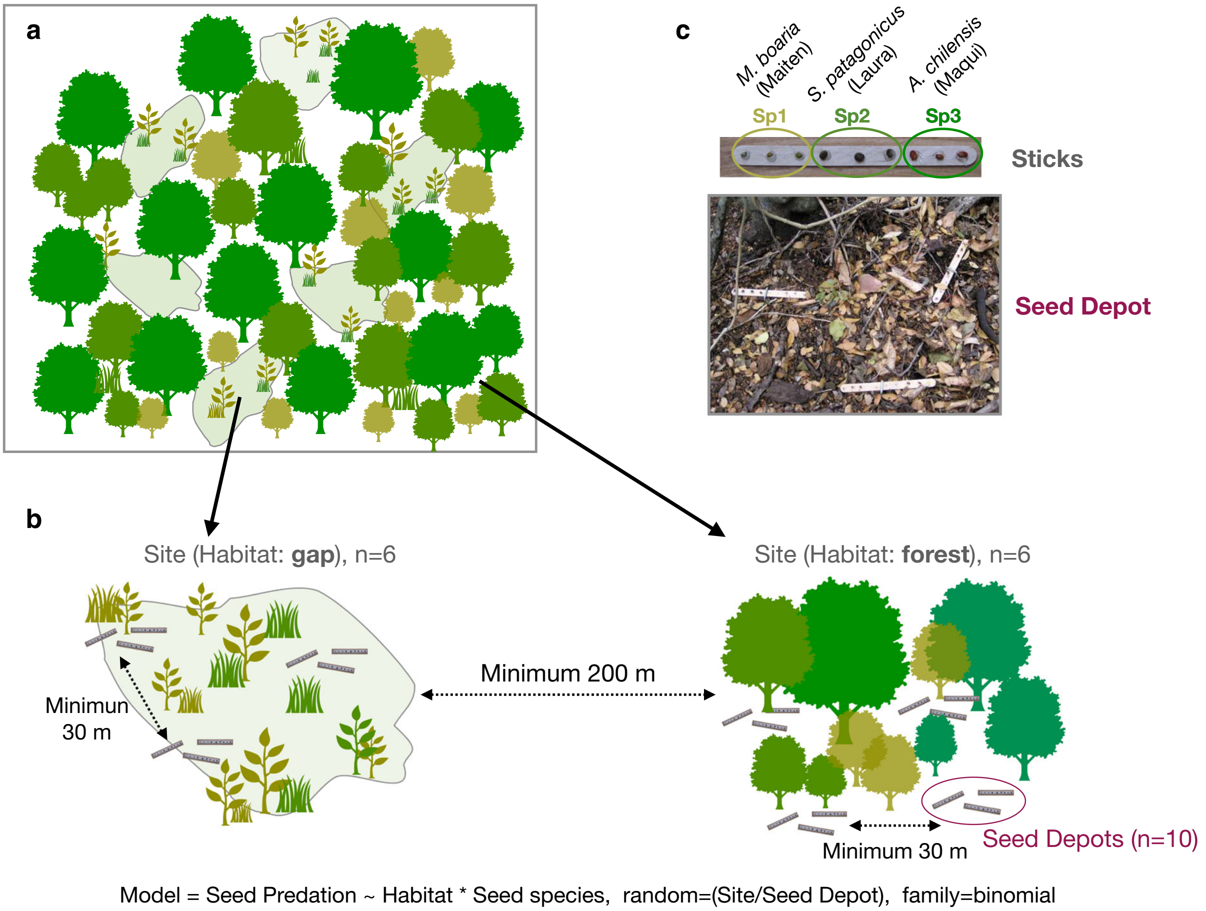

Fig. 1 Schematic representation of experimental design, and model construction (please see "Methods" section): **a**, **b** Forest gap array, number of sites, replicates, and model description; **c** popsicle sticks with seeds attached and depot arrangement

different gaps immersed in a large native forest, we tested and corroborated there were no differences among gap sites using a factorial analysis (Table S1). Finally, since sticks within each depot are pseudoreplicates, we used "seed depot" nested in "sites" as a random variable (Fig. 1). During monitoring, we found variable numbers of seed depots (minimum $n = 3$, maximum $n = 10$; blown, broken, or lost), but GLMMs contemplate uneven number of pseudoreplicates. To study the amount of total variation explained by each model, we used analysis of deviance (*pseudo r2*, BaylorEdPsych package; Beaujean 2012). Additionally, we performed a False Discovery Rate (FDR) post hoc test (Benjamini and Hochberg 1995) to compare the proportion of predation among seed species. All analyses were performed using R 3.5.0 (R Development Core Team 2018).

Results and discussion

We found that seed predation by rodents differed between habitats and, independently, between seed species, as shown by the non-significant interaction between factors (Table 1; Fig. 3b; Table S2). Seed predation was more than 2 × higher in forest gaps than in forest interior ($P < 0.001$, Table 1; Fig. 2).

Table 1 Anova of global factors' effects and GLMM results

Global fixed effects	Chisq	Df	*P* value	(pseudo) *r*2
Habitat	9.945	1	**0.001**	0.40
Seed species	11.355	1	**0.003**	
Habitat*seed species	0.742	2	0.689	

Statistically significant values are in bold

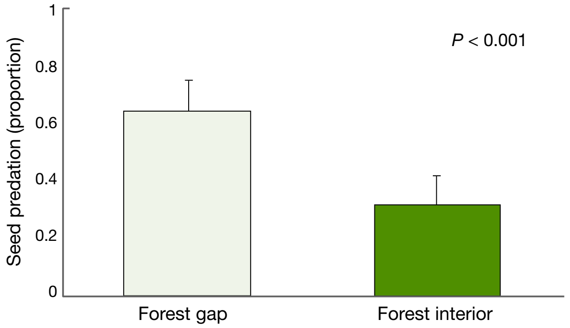

Fig. 2 Seed predation was higher in forest gaps. Proportion of seed predation in forest gap and forest interior after 48 h of field exposure. Letters mean significant difference between treatments ($p < 0.05$); bars represent means ± standard error

This result may seem counterintuitive, given that higher seed consumption in areas such as gaps would contradict “predation fear” behavior (Bleicher 2017). Several studies show evidence that rodents prefer to forage in sheltered habitats providing refuge from predators (Kollman and Buschor 2003; Yang et al. 2016; Zhang et al. 2016). For example, Germain et al. (2013) showed that seed predation varied spatially as seed predation decreased with decreasing vegetation cover. Yet, this behavior might vary among individuals (McArthur et al. 2014) and also can be influenced by the context (Steele et al. 2015) and the spatial scale considered (García et al. 2011). For instance, the ability of some species to accurately perceive changes in predation risk (Sundell et al. 2004) and the presence of other factors constraining foraging behavior (e.g., strong intra e interspecific competition; Yunger et al. 2002; Dupuch et al. 2014) might lead rodents to forage in riskier habitats. Maybe the fact that the ´seeds are there (in the sticks) make them more visible and available for the rodents. Because of the short period that seeds were exposed (Díaz et al. 1999), we assume that consumers were efficient in finding the seeds offered. Why rodents make the tradeoff of searching for good food in risky places is probably related to the fact that good food in safe places is harder to find (McArthur et al. 2014). On the other hand, although forest gaps from our study almost lacked tree canopy cover, they did present understory vegetation (see *Study area* section), which has shown to enhance seed predation rates (Kollman and Buschor 2003), as rodents suffer higher predation risk in areas with reduced vegetation cover of low height (Booman et al. 2009; Pons and Pausas 2007). Such a positive effect on seed predation has been in fact, previously reported for bamboo patches in forest gaps of the temperate Patagonian region (Caccia et al. 2006). Complementarily, habitat differences may emerge from a higher availability of fruits and seeds in forest gaps compared to forest interior, leading to positive responses among seed predators (García et al. 2011). Thus, although the present study does not enable us to discern a specific mechanism, we assume that both perception of risk and resource availability are underpinning the present habitat effects on seed predation.

Besides higher predation in gaps than in forests, we also found that the proportion of predated seeds depended on seed identity rather than on seed size (Table 1, Fig. 3a, b). The biggest seed species (*S. patagonicus*) was 41% and 17% more predated than medium-sized seed species (*M. boaria)* (P < 0.05) and the smaller ones, *A. chilensis* (P = 0.305),

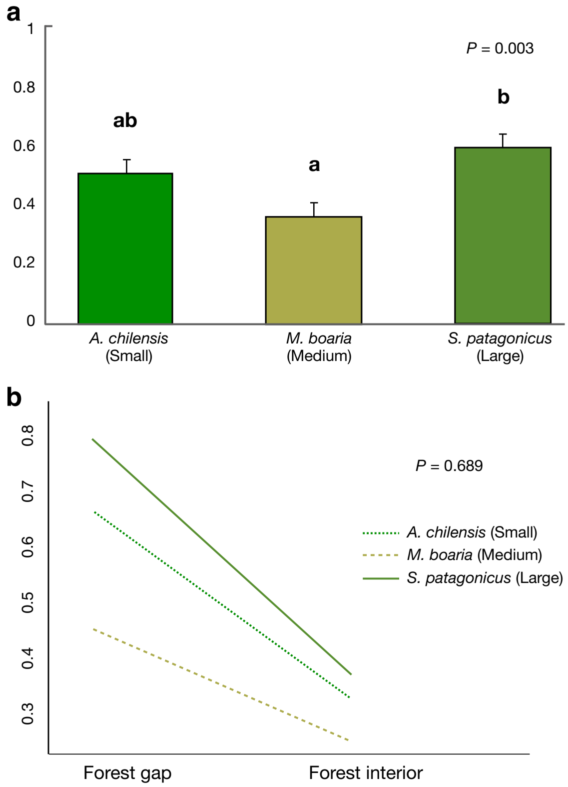

Fig. 3 *S. patagonicus* and *A. chilensis* were more predated regardless of habitat. **a** Average predation (proportion) of each seed species during the experiment. Letters mean significant difference among treatments ($p < 0.05$); bars represent means ± standard error; **b** Non-significant interaction between seed species and habitat

respectively (Fig. 3; Supp. Mat., Figure S1, Table S3). In addition, we found no differences on the proportion of predated seeds between *M. boaria* and *A. chilensis* (P = 0.101, Fig. 3; Figure S1, Table S3). Although seed traits promoting foraging behavior of rodents are controversial (Dylewski et al. 2020), several authors found that rodents prefer larger and heavier seeds (Nuñez et al. 2008; Carrillo-Gavilán et al. 2010; Chen et al. 2017; Wang and Ives 2017). However, consumption differences in our experiment mostly emerged between *S. patagonicus* and the intermediate-sized *M. boaria,* suggesting that size is not the only seed trait determining rodent choices. In any case, by making such "choices," rodents can generate interspecific differences in recruitment potential and influence forest regeneration dynamics (García et al. 2005; Larios et al. 2017 and references therein; Hegstad and Maron 2019; Moyano et al. 2019). Whether seed predation by rodents will finally leave an imprint in the composition of forest gaps will ultimately depend on the specific responses of seed species to other post-dispersal forces (drought, frost, and light tolerances, e.g., Manríquez et al. 2016; Promis and Allen 2017).

Our results on habitat and seed species effects on seed survival are based on a short-term, single estimation of seed predation, precluding somehow our ability to infer long-term and large-scale predictable patterns (see also Caccia et al. 2006). This is especially true in the case of interspecific differences in seed predation, which may be affected by the occurrence of seed masting events, especially from the highly erratic and low-frequency masting tree (e.g., *Nothofagus dombeyi*) or understory species (e.g., *Chusquea culeou*; Kitzberger et al. 2007). In spite of this, none of these plant species was masting in the year of our study, suggesting that our results may be at least extrapolated to the non-masting years. Regarding seasonal variability, it is also known that differential seed predation may change according to the variable proportion of different species in the seed rain or to increasing rodent densities (e.g., Díaz et al. 1999; but see Kollmann et al. 1998). In our case, we set up our experiment in the co-occurring peak of the fruiting season of the three fleshy-fruited plants under study, and thus our findings relate to the maximum potential densities of these seed species in the field. Concerning the spatial extent of our findings, we consider it to represent one of the main environmental conditions in forest ecosystems: forest vs. gaps. In fact, our additional factorial analysis revealed that predation rates were similar across gaps (Table S1), suggesting that the strong inter-habitat differences found here are generalized across the forest landscape.

Understanding how foraging activity of post-dispersal seed predator changes according to habitat patchiness and seed species identity is essential given their influence on forest composition and its regeneration process (Côté et al. 2003; Caccia et al. 2006; Bricker et al. 2010; Hegstad and Maron 2019). Yu et al. (2014) tested whether rodent seed predation or dispersal was beneficial for gap regeneration, and found that scatter-hoarding rodents rarely retrieved seeds from forest gaps, suggesting that rodent seed predation patterns contributed to the regeneration of the dominant species in gaps. In our case, the higher seed predation found in forest gaps might negatively impact on the recruitment of seedlings and slow down the forest regeneration of certain species. Our study then remarks the importance of considering species identity, given the fact that our results cannot be explained based on seed mass/size, and reinforce the idea that factor-associated habitat use by rodents at multiple spatial scales are important in mediating composition and regeneration of temperate southern forest communities.

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Availability of data and material See Supplementary Material.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Consent to participate All persons entitled to authorship have been so named.

Consent for publication All authors have approved its submission for publication in Plant Ecology.

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