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3 **POST DISPERSAL SEED PREDATION IN PATAGONIA TEMPERATE FOREST DEPENDS**  
4 **ON HABITAT PATCHINESS AND SEED SPECIES**  
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32 **ABSTRACT**

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

45  
46 **KEYWORDS:** rodent seed predators, cafeteria experiment,, habitat features, seed species.

47  
48 **DECLARATIONS**

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53 **Conflicts of interest/Competing interests**

54 Authors declare no conflict of interests

55 **Availability of data and material**

56 See Supplementary Material

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60 Not applicable

61 **Consent to participate**

62 All persons entitled to authorship have been so named

63 **Consent for publication**

64 All authors have approved its submission for publication in Plant Ecology

65 **Authors' contributions**

66 DG, GCA and MAR-C conceived the study and carried out fieldwork. LM and AV conducted the  
67 analyses and led the writing. All authors contributed substantially to the development of this  
68 manuscript, contributed critically to the drafts and gave final approval for publication.

69

70

71 **REMARK ABSTRACT**

72 • We aimed to investigate how forest habitat (forest interior vs. forest gaps) and seed species influence  
73 post dispersal seed predation.

74

75 • Patagonian temperate forests.

76

77 • We assessed consumption by rodents on three different native seed species in forest interior and forest  
78 gaps, by performing a cafeteria-style experiment.

79

80 • Seed predation was more than 2x higher in forest gaps than in forest interior, and medium sized seed  
81 species were the least preyed-upon.

82

83 • Understanding how forest habitat heterogeneity and seed species affect seed predation is fundamental  
84 to understand plant community dynamics in forest ecosystems.

85

## 86 INTRODUCTION

87

88 Post dispersal seed predation is a key process regulating plant population dynamics and  
89 community composition (Hulme 1998; Bricker et al. 2010; Maron et al. 2012; Hegstad and Maron  
90 2019). Seed predation can be highly variable and influenced by multiple factors including seed predator  
91 abundance and behavior (Orrock et al. 2010), habitat characteristics and seed traits (Kollman and  
92 Buschor 2003; García and Chacoff 2007; Moyano et al. 2019; Dylewski et al. 2020). Theory posts that  
93 while foraging, rodents should avoid low-quality food patches in favor of high-quality ones  
94 (MacArthur and Pianka 1966) and seek for safe patches while avoiding risky ones (the “foraging  
95 dilemma”, McArthur et al. 2014). On the one hand, habitats with complex structure can enhance  
96 rodents foraging activity by offering shelter from predators (Morris and Davidson 2000; Kollman and  
97 Buschor 2003). For example, habitat variables such as substrate and distance to nearest tree in  
98 Mediterranean forests (Fedriani 2005), and grass and shrub cover in temperate northern forests  
99 (Kollman and Buschor 2003) have better explained seed predation by rodents than seed phenotypic  
100 traits. In temperate forest ecosystems, understory cover and patchiness have shown to be relevant in  
101 driving seed predation patterns (Abe et al. 2001; Schnurr et al. 2004). On the other hand, seed traits  
102 such as mass (Jansen et al. 2004), size (Dylewski et al. 2020) and volume (Moyano et al. 2019), have  
103 explained rodents preference for seeds. Therefore, because food preference (i.e. seed selection) can  
104 interact with or overcome habitat features such as vegetation characteristics (Pons and Pausas 2007;  
105 Booman et al. 2009; García et al. 2011) integrating both is important for a better understanding of the  
106 processes that drive plant community structure (Larios et al. 2017).

107

108 Patchiness or forest cover variations are fundamental drivers of diversity and community dynamics in  
109 forest ecosystems (e.g., Jackson and Wong 1994; Schnurr et al. 2004; Heinemman et al. 2006; Ushio et  
110 al. 2010; Echeverria et al. 2014). Particularly, the regeneration and persistence of tree species in  
111 southern temperate forests can depend on forest-clearing dynamics (Veblen 1985; Bustamante &  
112 Armesto 1995; Pollmann 2003). Gutiérrez et al. (2004) found that small-scale disturbances (e.g., tree-  
113 fall originated gaps) increased the heterogeneity of the forest floor, producing microsites that favor the  
114 coexistence of plants with different regeneration modes. Also, in forest gaps, seeds previous to  
115 perturbation or seeds coming from adjacent patches are important for native vegetation to recover  
116 (Armesto et al. 2001; Parkes et al. 2003; Guidetti et al. 2016). In this context, it is known that forest  
117 cover variation can alter plant-animal interactions such as seed predation (Schnurr et al. 2004; Caccia et  
118 al. 2006; Royo and Carson 2008) which can vary among habitats in response to biotic effects (e.g.,

119 direct and indirect predator cues; Sivy et al. 2011) or environmental drivers (e.g., vegetation context,  
120 Booman et al. 2009; Pons and Pausas 2007; moonlight, Kotler et al. 2010). Therefore, it is reasonable  
121 to expect that habitat change alter seed predation patterns (Diaz et al. 1999; García and Chacoff 2007),  
122 which in turn can influence forest composition and regeneration (Schreiner et al. 2000; García et al.  
123 2005; Caccia et al. 2006).

124

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

130

## 131 **METHODS**

132

### 133 *Study area*

134 Our study was conducted in Llao-Llao Reserve, a 1220 ha area within Nahuel Huapi National Park in  
135 Patagonia – Argentina (41° 03 S, 71° 30 W), in Autumn 2005. Regional climate is humid in autumn-  
136 winter and dry in spring-summer, with 9°C average annual temperature and 1800 mm average annual  
137 precipitation (Cabrera 1976). The native forest vegetation belongs to the Subantarctic biogeographical  
138 region (Cabrera 1976), the dominant tree species being the evergreen southern beech (*Nothofagus*  
139 *dombeyi*) and cordilleran cypress (*Austrocedrus chilensis*) (Mermoz and Martín 1986). Llao-Llao  
140 Reserve has been protected since the 1960's but it was previously logged in certain areas, and canopy  
141 gaps of variable size have been generated by tree falls, giving the forest a patchy distribution (Amico et  
142 al. 2008). These gaps present some of the common understory vegetation dominated by the native  
143 shrub *Aristotelia chilensis* and native bamboo (*Chusquea culeou*) (Mermoz and Martín 1986). The  
144 main post-dispersal seed predators in the area are Cricetidae rodents (~25 gr.) such as the long-haired  
145 grass mouse (*Abrothrix hirta*), long-tailed mouse (*Oligoryzomys longicaudatus*) and olive grass mouse  
146 (*A. olivacea*) (Caccia et al. 2006; Nuñez et al. 2008; García et al. 2011). So far, there are no reports of  
147 scatter-hoarding rodents, and the authors found no evidence of bird seed predation (no removed soiled  
148 or bird excrements around seed depots). As the experiment was during Autumn, invertebrate or insect  
149 predation can be negligible.

150

### 151 *Cafeteria experiment*

152 In order to study if post dispersal seed predation varied between forest interior and forest gaps  
153 (“habitat”) and if there was a preference for different seeds (“species”) we established a cafeteria-style  
154 experiment (Lobo et al. 2009; Pearson et al. 2014; Moyano et al. 2019). We selected 6 forest gap sites  
155 distributed haphazardly inside the Llao-Llao Reserve, and 6 intact native forest interior sites, with gap  
156 and forest habitats differenced by the occurrence of tree canopy cover, forest having > 80% and gaps <  
157 10% (see Figure 1a for a schematic representation). As for seeds, we chose the three most common  
158 understory native species in these forests (García et al. 2011) and their seeds represent an optimal  
159 gradient of size/mass, from larger to smaller: *Schinus patagonicus* ( $18.81 \text{ mm}^2 \pm 0.21 \text{ mm}^2$ ;  $0.607 \text{ g} \pm$   
160  $0.019 \text{ g}$ ); *Maytenus boaria* ( $4.95 \text{ mm}^2 \pm 0.03 \text{ mm}^2$ ;  $0.368 \text{ g} \pm 0.029 \text{ g}$ ) and *Aristotelia chilensis* ( $3.25$   
161  $\text{mm}^2 \pm 0.02 \text{ mm}^2$ ;  $0.185 \text{ g} \pm 0.017 \text{ g}$ ) (Supplementary Material, Figure S1). These species are  
162 representative of the understory (as pioneers of clearing colonization); unaffected by masting behavior  
163 (enabling us to extrapolate to the medium-term), and endozoochorous (thus homogenizing the  
164 functional group and its implications in expected patterns of spatial distribution of deposition). Seeds  
165 were obtained from fruits randomly collected on plants at the study site, in order to estimate specific  
166 individual seed mass/size and to prepare a seed pool for experimental depots.

167

168 In the experiment, we offered seeds to predators in the field by attaching them to wooden popsicle  
169 sticks holding 3 seeds of each species (9 seeds total per stick, Figure 1c). Seeds were fastened to the  
170 sticks in a random order, using non-toxic glue, wearing gloves to prevent human scent to impregnate  
171 them (García et al. 2011). At each forest and gap sites, we randomly placed seed depots (=set of 3  
172 wooden popsicle sticks; Figure 1b, c) at a minimum distance of 25 cm each, nailed to the ground with a  
173 wire staple over each stick center. Because understory cover is an important factor influencing seed  
174 predation rate (Caccia et al. 2009; Royo and Carson 2008) we placed seed depots under parental  
175 species shrubs. This also controls for possible differences in real seed rain densities, usually expected to  
176 be stronger under bush, than far from bush (especially in clearings; García et al. 2011). Initially, 10  
177 seed depots were placed separated at least 30 m from each other, and sites were more than 200 m apart  
178 (Figure 1b). We evaluated seed predation after 48 hs of installing the experiment, a period comparable  
179 with previous studies in several environments (Hulme 1994; Kollman et al. 1998; Hulme & Borelli  
180 1999; Orrock 2015). Both the seeds removed from the popsicle sticks and those damaged (with obvious  
181 bite marks) but remaining in place were considered as predated.

182

183 *Statistical analyses*

184 To determine if seed predation (response variable) differed between “habitats” (“forest interior”, “forest  
185 gaps”) we used generalized mixed linear models (GLMM) (Figure 1). Seed predation was calculated as  
186 the proportion of predated seeds after 48 hs. To evaluate if there was a preference for seed “species” we  
187 included it as a predictive variable, with factors “Small” (*A.chilensis*), “Medium” (*M.boaria*) and  
188 “Large” (*S.patagonicus*). We also considered the interaction between factors, in order to test if potential  
189 differences between species depended on the habitat type. We assumed a binomial distribution, using a  
190 GLMM based on Laplace approximation and a logit link function (lme4 package, *glmer* function, Bates  
191 et al. 2015). Since our experimental design had different gaps immersed in a large native forest, we  
192 tested and corroborated there were no differences amongst gap sites using a factorial analysis (Table  
193 S1). Finally, since sticks within each depot are pseudo-replicates, we used “seed depot” nested in  
194 “sites” as a random variable (Figure 1). During monitoring, we found variable numbers of seed depots  
195 (minimum  $n = 3$ , maximum  $n = 10$ ; blown, broken o lost), but GLMM’s contemplate uneven number of  
196 pseudoreplicates. To study the amount of total variation explained by each model, we used analysis of  
197 deviance (*pseudo r2*, BabylonEdPsych package; Beaujean 2012). Additionally, we performed a False  
198 Discovery Rate (FDR) post hoc test (Benjamini and Hochberg 1995) to compare the proportion of  
199 predation among seed species. All analyses were performed using R 3.5.0 (R Development Core Team  
200 2018).

201

## 202 **RESULTS & DISCUSSION**

203

204 We found that seed predation by rodents differed between habitats and, independently, between seed  
205 species, as shown by the non-significant interaction between factors (Table 1; Figure 3b; Table S2).  
206 Seed predation was more than 2x higher in forest gaps than in forest interior ( $P < 0.001$ , Table 1;  
207 Figure 2). This result may seem counterintuitive, given that higher seed consumption in areas such as  
208 gaps would contradict “predation fear” behavior (Bleicher 2017). Several studies show evidence that  
209 rodents prefer to forage in sheltered habitats providing refuge from predators (Kollman and Buschor  
210 2003; Yang et al. 2016; Zhang et al. 2016). For example, Germain et al. (2013) showed that seed  
211 predation varied spatially as seed predation decreased with decreasing vegetation cover. Yet, this  
212 behavior might vary among individuals (McArthur et al. 2014) and also can be influenced by the  
213 context (Steele et al. 2015) and the spatial scale considered (García et al. 2011). For instance, the ability  
214 of some species to accurately perceive changes in predation risk (Sundell et al. 2004) and the presence  
215 of other factors constraining foraging behavior (e.g., strong intra e interspecific competition; Yunger et  
216 al. 2002, Dupuch et al. 2014) might lead rodents to forage in riskier habitats. Maybe the fact that the

217 'seeds are there (in the sticks)' make them more visible and available for the rodents. Because of the  
218 short period that seeds were exposed (Díaz et al. 1999), we assume that consumers were efficient in  
219 finding the seeds offered. Why rodents make the tradeoff of searching for good food in risky places is  
220 probably related to the fact that good food in safe places is harder to find (McArthur 2014). On the  
221 other hand, although forest gaps from our study almost lacked tree canopy cover, they did present  
222 understory vegetation (see *Study area* section), which has shown to enhance seed predation rates  
223 (Kollman and Buschor 2003), as rodents suffer higher predation risk in areas with reduced vegetation  
224 cover of low height (Booman et al. 2009; Pons and Pausas 2007). Such a positive effect on seed  
225 predation has been in fact, previously reported for bamboo patches in forest gaps of the temperate  
226 Patagonian region (Caccia et al. 2006). Complementarily, habitat differences may emerge from a higher  
227 availability of fruits and seeds in forest gaps compared to forest interior, leading to positive responses  
228 among seed predators (García et al. 2011). Thus, although the present study does not enable us to  
229 discern a specific mechanism, we assume that both perception of risk and resource availability are  
230 underpinning the present habitat effects on seed predation.

231

232 Besides higher predation in gaps than in forests, we also found that the proportion of predated seeds  
233 depended on seed identity rather than on seed size (Table 1, Figure 3a, b). The biggest seed species (*S.*  
234 *patagonicus*) was 41% and 17% more predated than medium-sized seed species (*M. boaria*) ( $P < 0.05$ )  
235 and the smaller, *A. chilensis* ( $P = 0.305$ ) respectively (Figure 3; Supp. Mat., Figure S1, Table S3). In  
236 addition, we found no differences on the proportion of predated seeds between *M. boaria* and *A.*  
237 *chilensis* ( $P = 0.101$ , Figure 3; Figure S1, Table S3). Although seed traits promoting foraging behavior  
238 of rodents are controversial (Dylewski et al. 2020), several authors found that rodents prefer larger and  
239 heavier seeds (Nuñez et al. 2008; Carrillo-Gavilán et al. 2010; Chen et al. 2017; Wang and Ives 2017).  
240 However, consumption differences in our experiment mostly emerged between *S. patagonicus* and the  
241 intermediate-sized *M. boaria*, suggesting that size is not the only seed trait determining rodent choices.  
242 In any case, by making such "choices", rodents can generate interspecific differences in recruitment  
243 potential and influence forest regeneration dynamics (García et al. 2005; Larios et al. 2017 and  
244 references therein; Hegstad and Maron 2019; Moyano et al. 2019). Whether seed predation by rodents  
245 will finally leave an imprint in the composition of forest gaps will ultimately depend on the specific  
246 responses of seed species to other post-dispersal forces (drought, frost and light tolerances; e.g.,  
247 Manríquez et al. 2016; Promis and Allen 2017).

248



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

265

266 Understanding how foraging activity of post-dispersal seed predator changes according to habitat  
267 patchiness and seed species identity is essential given their influence on forest composition and its  
268 regeneration process (Côté et al. 2003, Caccia et al. 2006; Bricker et al. 2010, Hegstad and Maron  
269 2019). Yu et al. (2014) tested whether rodent seed predation or dispersal was beneficial for gap  
270 regeneration, and found that scatter-hoarding rodents rarely retrieved seeds from forest gaps,  
271 suggesting that rodent seed predation patterns contributed to the regeneration of the dominant species  
272 in gaps. In our case, the higher seed predation found in forest gaps might negatively impact on the  
273 recruitment of seedlings and slow down the forest regeneration of certain species. Our study then  
274 remarks the importance of considering species identity, given the fact that our results cannot be  
275 explained based on seed mass/size, and reinforce the idea that factors associated habitat use by rodents  
276 at multiple spatial scales are important in mediating composition and regeneration of temperate  
277 southern forest communities.

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474 **TABLES**

475

476 **TABLE 1.** Anova of global factors effects and GLMM results. Statistically significant values are in bold.

<b>Global fixed effects</b>	<b>Chisq</b>	<b>Df</b>	<b>P value</b>	<b>(pseudo) r<sup>2</sup></b>
Habitat	9.945	1	<b>0.001</b>	0.40
Seed Species	11.355	1	<b>0.003</b>	
Habitat*Seed Species	0.742	2	0.689	

477



478 **FIGURES**

479

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

483

484 **Fig 2 Seed predation was higher in forest gaps.** Proportion of seed predation in forest gap and forest  
485 interior after 48 hours of field exposure. Letters mean significant difference between treatments ( $p <$   
486 0.05); bars represent means  $\pm$  standard error.

487

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

491

Figure 1a

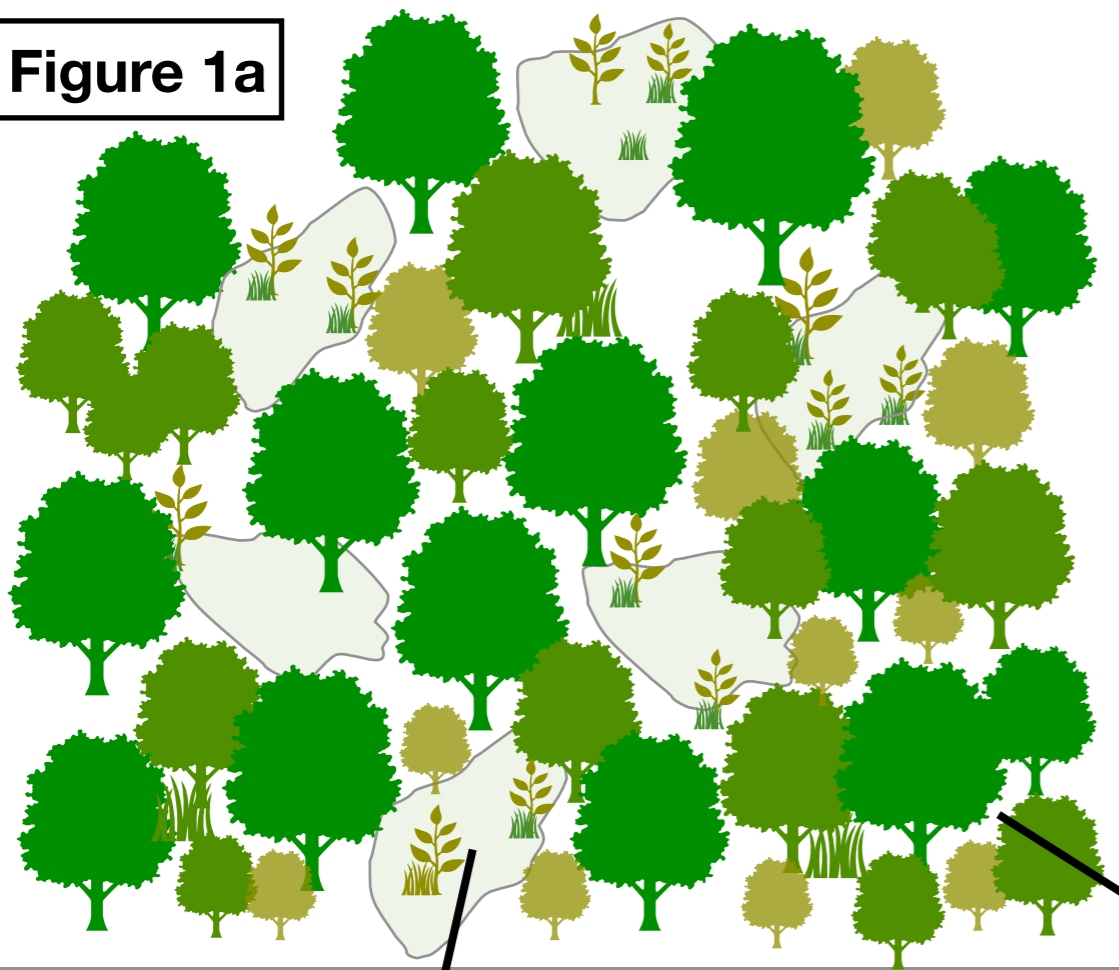


Figure 1c

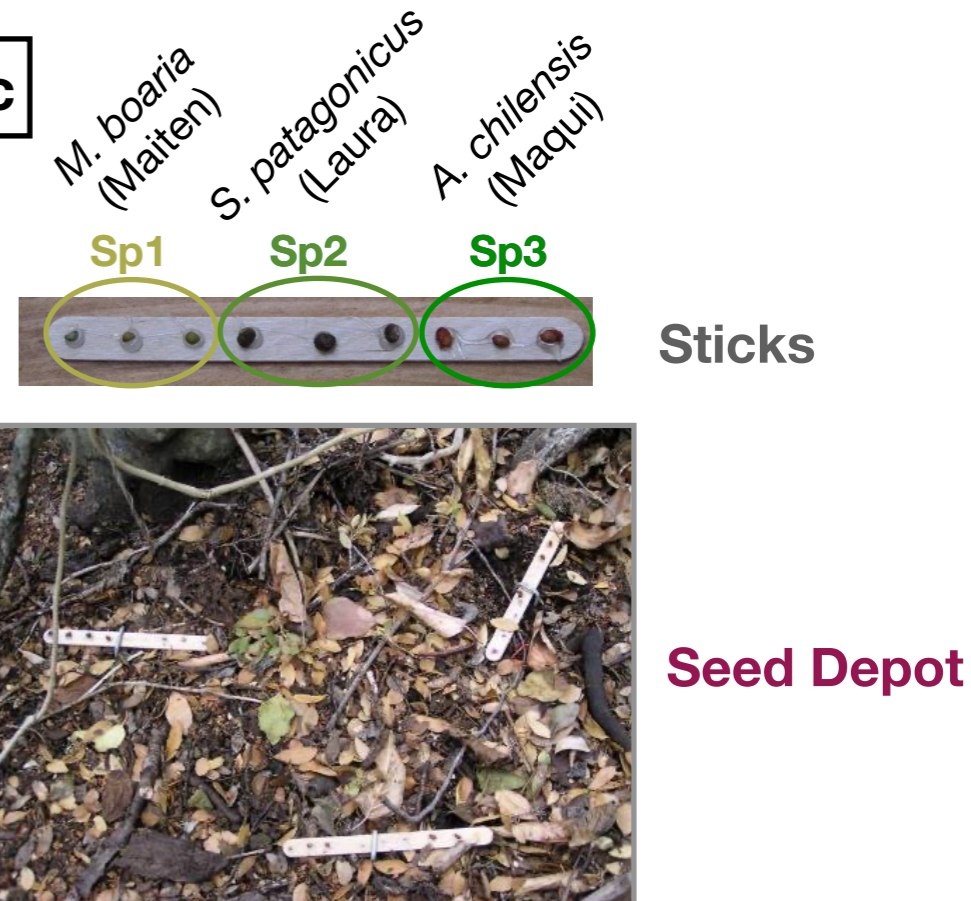
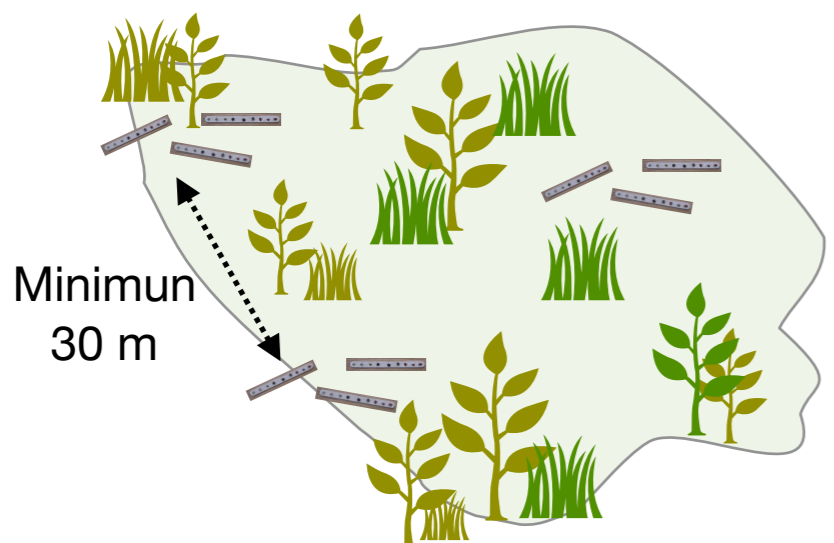
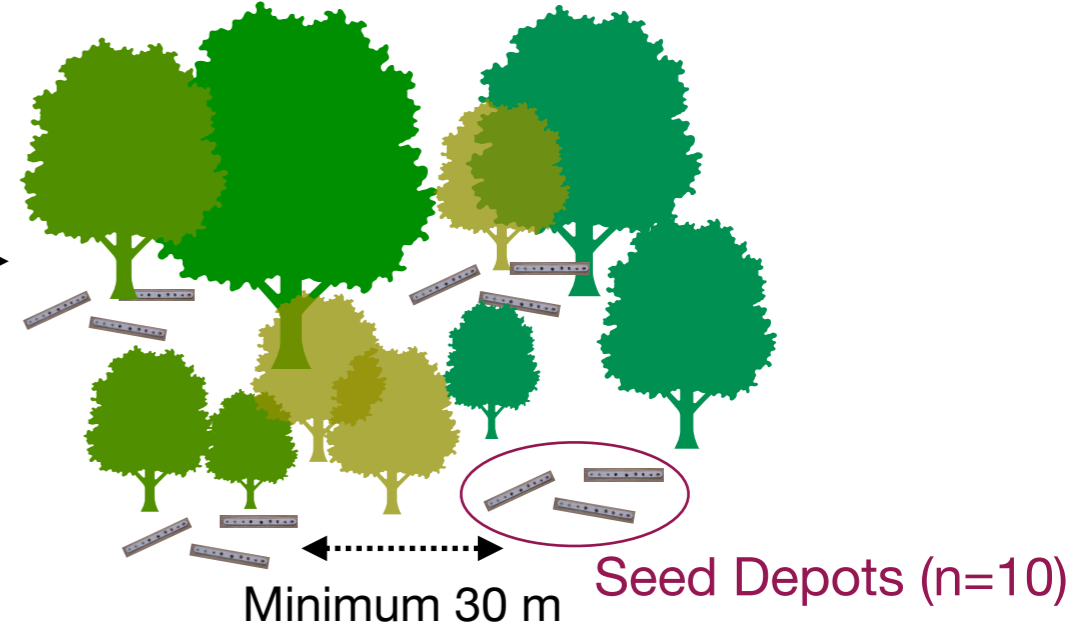


Figure 1b

Site (Habitat: **gap**), n=6

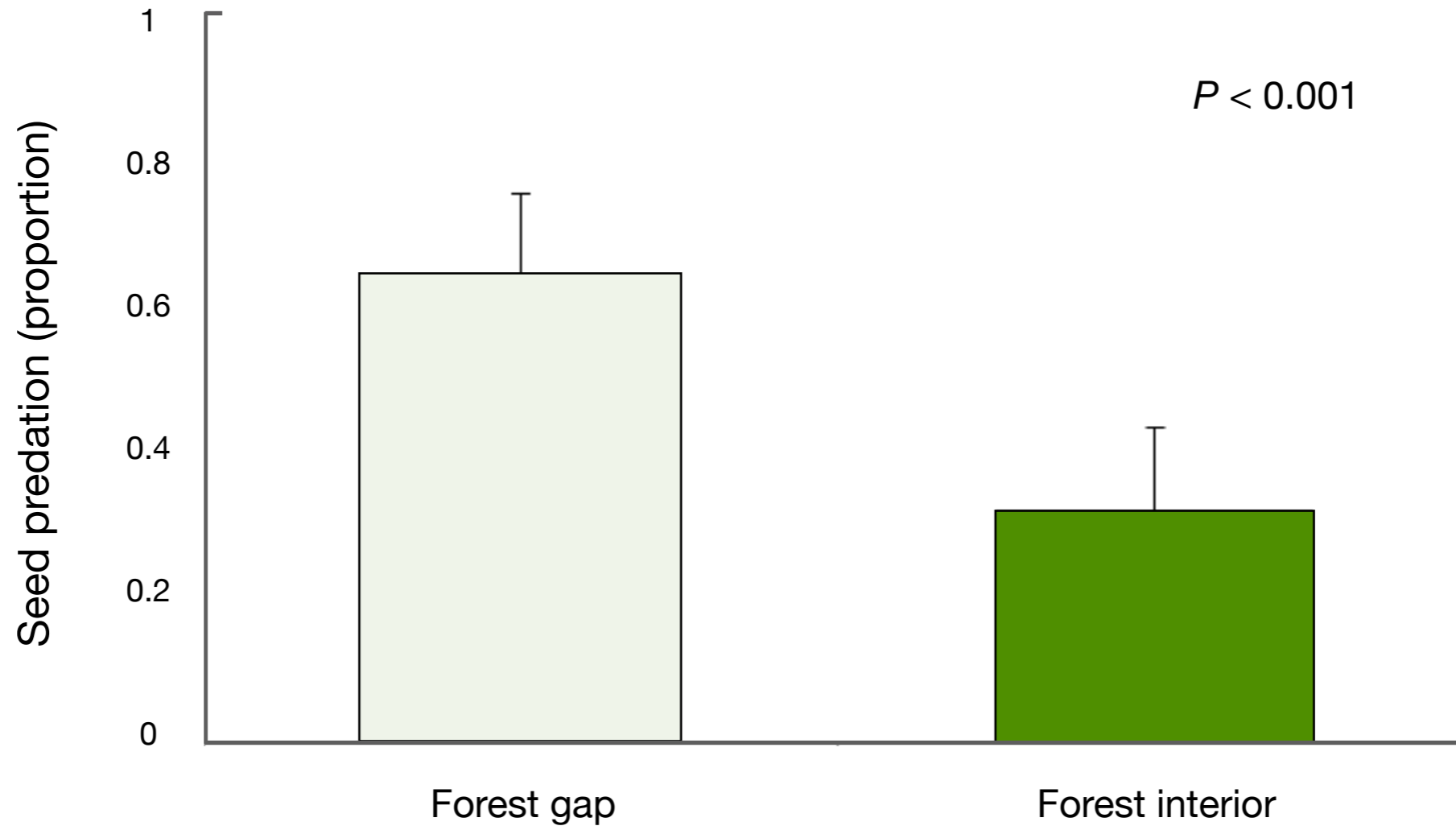


Site (Habitat: **forest**), n=6

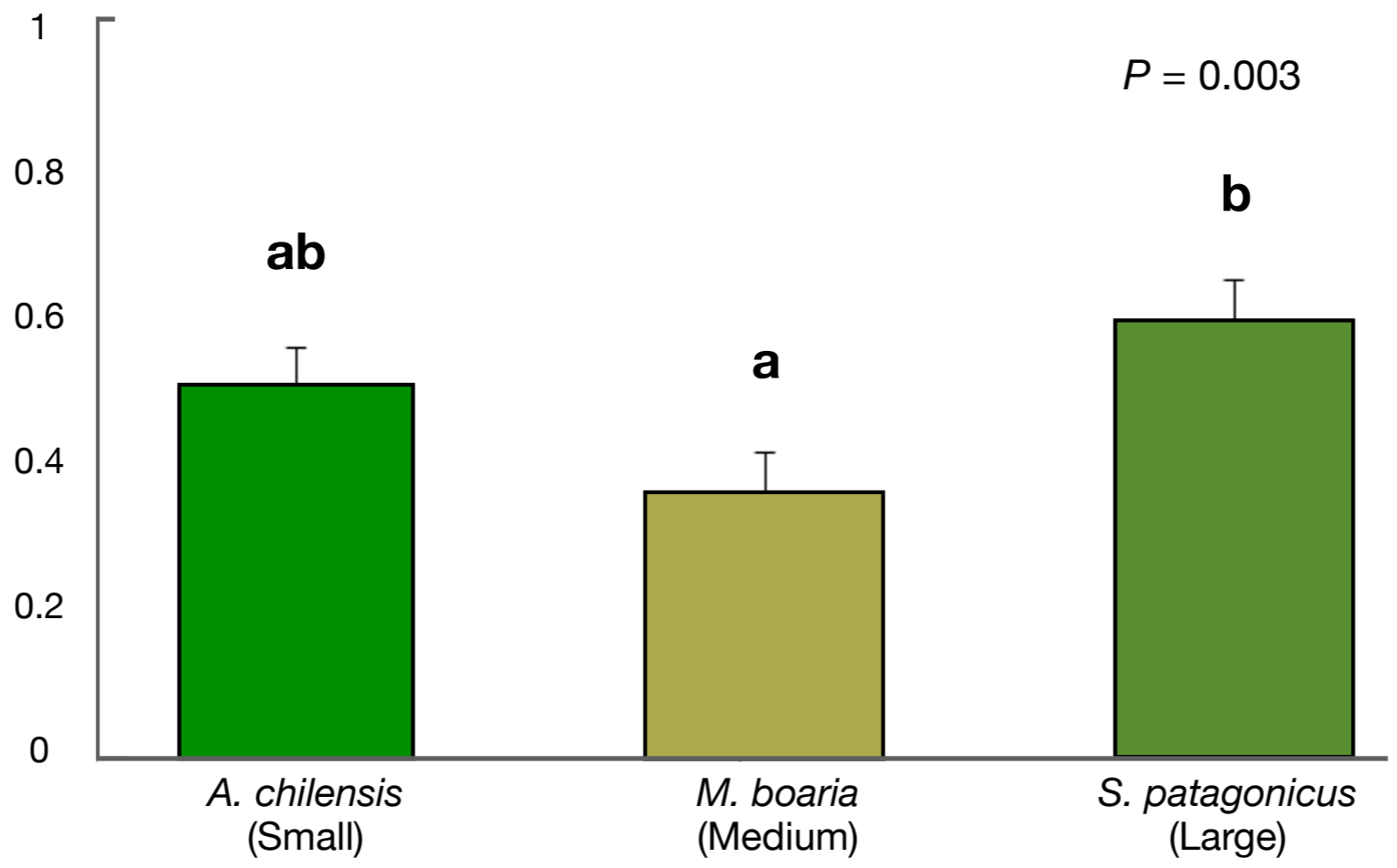


Model = Seed Predation ~ Habitat \* Seed species, random=(Site/Seed Depot), family=binomial

**Figure 2**



**Figure 3a**



**Figure 3b**

