



## 17 **Summary**

- 18 1. Identification of the mechanisms enabling stable coexistence of species with  
19 similar resource requirements is a central challenge in ecology. Such coexistence  
20 can be facilitated by species at higher trophic levels through complex multi-  
21 trophic interactions, a mechanism that could be compromised by ongoing  
22 defaunation.
- 23 2. We investigated cascading effects of defaunation on *Pachymerus cardo* and  
24 *Speciomerus giganteus*, the specialized insect seed predators of the Neotropical  
25 palm *Attalea butyracea*, testing the hypothesis that vertebrate frugivores and  
26 granivores facilitate their coexistence.
- 27 3. Lab experiments showed that the two seed parasitoid species differed strongly in  
28 their reproductive ecology. *Pachymerus* produced many small eggs that it  
29 deposited exclusively on the fruit exocarp (exterior). *Speciomerus* produced few  
30 large eggs that it deposited exclusively on the endocarp, which is normally  
31 exposed only after a vertebrate handles the fruit. When eggs of the two species  
32 were deposited on the same fruit, *Pachymerus* triumphed only when it had a  
33 long head start, and the loser always succumbed to intraguild predation.
- 34 4. We collected field data on the fates of 6569 *Attalea* seeds across sites in central  
35 Panama with contrasting degrees of defaunation and wide variation in the  
36 abundance of vertebrate frugivores and granivores. *Speciomerus* dominated  
37 where vertebrate communities were intact, whereas *Pachymerus* dominated in  
38 defaunated sites. Variation in the relative abundance of *Speciomerus* across all  
39 84 sampling sites was strongly positively related with the proportion of seeds  
40 attacked by rodents, an indicator of local vertebrate abundance.
- 41 5. Synthesis: We show that two species of insect seed predators relying on the  
42 same host plant species are niche differentiated in their reproductive strategies  
43 such that one species has the advantage when fruits are handled promptly by  
44 vertebrates and the other when they aren't. Defaunation disrupts this mediating  
45 influence of vertebrates and strongly favors one species at the expense of the  
46 other, providing a case study of the cascading effects of defaunation and its  
47 potential to disrupt coexistence of non-target species, including the hyperdiverse  
48 phytophagous insects of tropical forests.

49 **Key-words:** *Attalea butyracea*, facilitation, intraguild predation, multi-trophic  
50 interactions, Panama, seed fate, seed beetles, top-down control, trophic cascades.

51

## 52 **Introduction**

53 Identification of the mechanisms that enable the coexistence of species with similar  
54 resource requirements is fundamental for understanding the organization and  
55 maintenance of biodiversity. This challenge has traditionally been addressed by  
56 focusing on antagonistic interactions in just one (competition) or two (predator-prey)  
57 trophic levels (Gurevitch, Morrison & Hedges 2000; Chase *et al.* 2002). However, the

58 recognition of intraguild predation, i.e. competitors killing and eating each other (Arim  
59 & Marquet 2004) and facilitative interactions as important community structuring  
60 forces (Bruno, Stachowicz & Bertness 2003) has fostered the adoption of more holistic  
61 multi-trophic approaches (Tscharrntke & Hawkins 2002; Smith, Mooney & Agrawal  
62 2008; Visser *et al.* 2011). Further, interspecific interactions may show conditionality  
63 when their net outcome varies with the ecological context (Bronstein 1994). The  
64 heterogeneity of natural communities thus requires studying species coexistence in  
65 contrasting multi-trophic contexts to disentangle the effects of the antagonistic and  
66 facilitative mechanisms (Amarasekare 2008).

67 Phytophagous insects provide paradigmatic cases of species that coexist despite  
68 similar resource requirements. Seed predators in particular are a diversified guild of  
69 insects that often show high degrees of niche overlap due to their high levels of host-  
70 specificity (Janzen 1980; Novotny & Basset 2005; Delobel & Delobel 2006).  
71 Competing seed parasitoid species are typically differentiated in their adult phenologies  
72 and oviposition behaviors (Mitchell 1975; Messina 1991; Johnson & Romero 2004;  
73 Espelta, Bonal & Sánchez-Humanes 2009). Yet, despite these differences, a single seed  
74 may end up with larvae of more than one species (Espelta *et al.* 2009). Seeds are  
75 discrete resources, which sometimes cannot sustain the development of more than one  
76 individual, and thus larval competition within a seed is intense. One of the usual  
77 outcomes of such competition is intraguild predation among larvae leaving a single  
78 survivor (Wilson & Janzen 1972; Janzen 1975; Traveset 1991; Peguero, Bonal &  
79 Espelta 2014). Though such direct interspecific competition is clearly important, a  
80 community-wide perspective is needed to account for indirect, enemy-mediated and  
81 facilitative effects across different trophic levels (Kaplan & Denno 2007).

82 Coexistence between species that share the same key resource could be stabilized if  
83 the outcome of their competition varies with the community context (Smith *et al.* 2008).  
84 In the case of insect seed predators sharing the same host plant, variation in the  
85 abundance of another seed consumer or shared enemy can modulate their intraguild  
86 competition if one of the insects is more vulnerable to or favored by this third agent. For  
87 instance, one insect could dominate its competitor in the presence of a facilitative  
88 species, but be subordinate in its absence. Variation in relative dominance would then  
89 result from this third species disproportionately favoring the inferior competitor and/or  
90 disadvantaging the superior competitor. If the abundance of the third species is spatially  
91 heterogeneous, the coexistence of competing species at a regional level could be  
92 stabilized (see Gurevitch *et al.* 2000 and Chase *et al.* 2002 for a similar reasoning for  
93 competitors under variable predation pressure). However to our knowledge, the  
94 hypothesis that multi-trophic interactions may mediate the coexistence of specialized  
95 seed predators has never been empirically tested.

96 Vertebrates are key candidates for mediating the coexistence of seed predators, as  
97 they may feed on the fruits and seeds as well as on larvae inside fruits and seeds  
98 (Sallabanks & Courtney 1992). Examples of top-down control by reptiles, birds and  
99 mammals of insect species at lower trophic levels are many (Terborgh *et al.* 2001;  
100 Böhm, Wells & Kalko 2011; Visser *et al.* 2011), but we know of no study that has

101 considered whether vertebrates facilitate the coexistence of competing insects such as  
102 specialized seed predators. The question of whether or not vertebrates mediate insect  
103 species coexistence is particularly important given the diversity of insects combined  
104 with global defaunation trends, i.e., the extirpation and population decline of native  
105 vertebrate species, which can increase the variability of local abundances producing  
106 many unanticipated cascade effects of biodiversity loss (Dirzo *et al.* 2014).

107 Here, we study the consequences of defaunation for species coexistence by assessing  
108 whether and how vertebrate frugivores and granivores affect the competitive balance of  
109 two specialized bruchid beetles (Bruchinae: Pachymerini) whose larvae are seed  
110 predators of the tropical palm *Attalea butyracea* (hereafter ‘*Attalea*’). Previous studies  
111 suggested that these bruchids differ in oviposition strategy. The larger species –  
112 *Speciomerus giganteus* (hereafter ‘*Speciomerus*’) – lays its eggs on exposed endocarps  
113 on the forest floor, and is thus a post-dispersal seed parasitoid (Wright 1983). The  
114 smaller species – *Pachymerus cardo* (hereafter ‘*Pachymerus*’) – is thought to lay its  
115 eggs on the exocarp of the fruits while they are developing in the canopy, and would  
116 thus be a pre-dispersal seed parasitoid, like its local sister species *P. bactris*, the seed  
117 parasitoid of the palm *Astrocaryum standleyanum* (Jansen *et al.* 2010). Though multiple  
118 larvae usually infest the same seed, only one adult bruchid can emerge, suggesting that  
119 intraguild predation occurs among bruchid larvae (Wilson & Janzen 1972; Wright  
120 1983).

121 Vertebrates may affect these bruchids in at least three ways (Fig. 1). First, many  
122 vertebrate species feed on the fruit pulp, thus exposing the endocarp to oviposition by  
123 *Speciomerus*. Second, three species of rodents remove and store seeds as food supplies  
124 in shallow soil-surface caches, thus moving seeds out of reach of bruchids (Jansen *et al.*  
125 2010, 2012, 2014). Third, at least two rodent species also consume bruchid larvae  
126 (Silvius & Fragoso 2002; Gálvez & Jansen 2007) and may exert a strong top-down  
127 control over bruchid populations (Wright & Duber 2001; Visser *et al.* 2011). Previous  
128 studies monitoring fruit falling into traps showed that 63% of the fruits have their  
129 endocarps partly exposed (n = 2468, 21 palms) on Barro Colorado Island, which has a  
130 complete vertebrate community, versus just 18% (n = 5270, 27 palms) in Soberania  
131 National Park which has high levels of poaching (P.A. Jansen, unpublished data). This  
132 suggests that the accessibility of *Speciomerus* to the endocarps is lower where frugivore  
133 populations are smaller, allowing more *Pachymerus* larvae to develop. Therefore, our  
134 overarching hypothesis was that vertebrates mediate the coexistence of these beetles,  
135 and that defaunation could favor one parasitoid at the expense of the other.

136 We tested the following specific predictions: (1) *Pachymerus* and *Speciomerus* differ  
137 importantly in reproductive ecology; (2) *Speciomerus* larvae kill *Pachymerus* larvae in  
138 the same seed, unless *Pachymerus* has a sufficiently long head start; and (3) relative  
139 abundances of the two species will depend on vertebrate abundance, with *Speciomerus*  
140 dominating where vertebrate frugivores are common, because the latter facilitate its  
141 oviposition and reduce the head start of *Pachymerus*. We tested these hypotheses  
142 through oviposition trials and competition experiments, combined with sampling at sites  
143 with contrasting vertebrate abundance. Overall, our results indicate that vertebrates

144 indeed mediate the coexistence of the specialized seed predators in this system by  
145 modifying their competitive balance. Thus, we demonstrate that multi-trophic  
146 interactions can contribute to the coexistence of insect species with similar resource  
147 requirements.

## 148 **Materials and Methods**

### 149 **Study system**

150 This study was carried out in central Panama, at Barro Colorado Island (BCI), in  
151 Soberania National Park (SNP), and at small (<1.5 ha) islands in Gatun Lake (hereafter  
152 referred to as islets). Annual rainfall averages 2600 mm with a distinct 4-month dry  
153 season from January to April. The vegetation is semi-deciduous tropical moist forest.  
154 Because BCI is well-protected from poaching while SNP is not, vertebrates are much  
155 more abundant on BCI than in SNP (Wright *et al.* 2000). The islets are virtually  
156 defaunated because they are too small to sustain populations of vertebrates larger than  
157 rats (Adler & Seamon 1991; Wright & Duber 2001). Thus, these three types of site form  
158 a gradient of defaunation.

159 *Attalea butyracea* (Mutis ex L.f.) Wess. Boer (formerly *Scheelea zonensis*) is a  
160 monoecious arborescent canopy or subcanopy palm that is abundant in Panama (Wright  
161 1983). Mature individuals annually produce one to three infructescences with 100-600  
162 ovoid drupes (3-6 cm length) that ripen during the first half of the wet season (Wright  
163 1983). These fruits have a tough exocarp, a soft oily mesocarp and a stone, i.e., a hard  
164 woody endocarp that usually encloses one seed, although around 2% contain two or  
165 even three seeds (Bradford & Smith 1977). The woody endocarps remain on the forest  
166 floor more than 3 years as they slowly decompose (Wright 1983). The mesocarp is  
167 eaten by many vertebrate species including Baird's tapir (*Tapirus bairdii* Gill), white-  
168 faced monkey (*Cebus capucinus* L.), howler monkey (*Alouatta palliata* L.), kinkajou  
169 (*Potos flavus* Schreber) and red-lored parrot (*Amazona autumnalis* L.), all of which are  
170 able to open the tough exocarp (Wright *et al.* 2000, G. Peguero, personal observation).  
171 Of these, only Baird's tapir ingests the endocarps (Jansen *et al.* 2014). Three rodent  
172 species – Red-tailed squirrel (*Sciurus granatensis* Humboldt), Central American agouti  
173 (*Dasyprocta punctata* Gray) and Central American spiny rat (*Proechimys semispinosus*  
174 Tomes) – are also able to open the endocarps to eat the seeds or the bruchid larvae  
175 inside (Wright & Duber 2001; Gálvez & Jansen 2007; Jansen *et al.* 2014).

176 Two bruchid beetles prey on *Attalea* seeds in this area: *Speciomerus giganteus*  
177 Chevrolat and *Pachymerus cardo* Fåhåreus (henceforth referred to by their genus  
178 names). They have no other local hosts (S. Gripenberg, pers. comm.) and no known  
179 larval predators (S.J. Wright, unpublished data). *Speciomerus* is larger and is a post-  
180 dispersal seed parasitoid that only lays eggs on defleshed endocarps, i.e. after opening  
181 or removal of the exocarp by a frugivore (Wilson & Janzen 1972; Wright 1983). In  
182 contrast, *Pachymerus* can lay its eggs directly on intact and partially de-fleshed fruits  
183 (Silvius & Fragoso 2002, D. Gálvez, unpublished data) hence could be a pre-dispersal  
184 seed parasitoid. Previous observations also suggest differences in fecundity traits like  
185 egg number and size (D. Gálvez, unpublished data). Relative abundance differs among

186 sites. *Speciomerus* is dominant in BCI (Visser *et al.* 2011) whereas *Pachymerus*  
187 accounts for more than half of bruchid emergences in the SNP (S.J. Wright,  
188 unpublished data).

## 189 **Reproductive ecology**

190 We quantified differences between the two bruchids in the timing of adult  
191 emergence, egg number and size, and oviposition site preferences. We collected 750  
192 endocarps beneath approximately 15 haphazardly selected trees along Pipeline Road in  
193 SNP during the dry season of 2013 and incubated them in 15 20-liter buckets sealed off  
194 with insect screening at ambient temperature but protected from rain and direct sunlight.  
195 Buckets were checked daily, the timing of emergence was recorded and each bruchid  
196 was identified to species. We evaluated interspecific differences in the timing of  
197 emergence using a generalized estimating equation model (GEE) with a Poisson log-  
198 link function that included the interaction between species and emergence time (in  
199 ordinal days), treated each incubation bucket as a blocking factor, and included an  
200 autoregressive correlation structure for each bucket (block) to account for the  
201 longitudinal nature of the data.

202 The emerged bruchids were mixed and placed in groups of 10-20 conspecifics in  
203 25×20×8 cm plastic containers with dry leaves and water in glass vials. After allowing  
204 for mating, 17 females of each species were placed individually in plastic containers  
205 with one intact fruit, one partially de-fleshed endocarp (i.e. a gashed fruit conserving  
206 half of the exo- and mesocarp) and a bare endocarp (i.e. a fruit with exo- and mesocarp  
207 completely removed). These treatments mimic the three most common levels of fruit  
208 handling by vertebrates: a non-handled fruit, an endocarp partially de-fleshed by a  
209 canopy-dwelling pulp feeder, and an endocarp entirely de-fleshed, as a scatter-hoarding  
210 rodent would do (Silvius & Fragoso 2002; Gálvez & Jansen 2007; Jansen *et al.* 2010).  
211 Fruits were mixed and randomly assigned to treatments to ensure that there were no  
212 differences in size or maturation stage.

213 Every 72 hours, the fruits were replaced by new ones (i.e. fruits collected and  
214 manipulated the same day). The number of eggs laid in each fruit treatment and whether  
215 they were attached to the exocarp or to the endocarp in the partially de-fleshed fruits  
216 was monitored daily until the beetles died. Interspecific differences in oviposition  
217 preference were inferred from the proportion of eggs laid on each fruit type and the  
218 proportion of eggs attached to endo- versus exocarp. We fitted generalized linear  
219 models (GLM) with binomial or, if overdispersed, quasibinomial errors, and with  
220 species as factor and lifetime as covariate, to assess potential behavioral differences  
221 related with maternal lifetime.

222 A random subsample of the eggs of six females per species ( $35 \pm 6$  eggs per female,  
223 mean  $\pm$  SE, N = 418) were photographed and their maximum length and width  
224 measured to the nearest 0.001 mm using the software ImageJ (Schneider, Rasband &  
225 Eliceiri 2012). Egg volume was calculated from these measurements under the  
226 assumption that the eggs were prolate spheroids, i.e., as  $(4\pi/3)a^2c$ , where  $a$  is the  
227 equatorial diameter and  $c$  is the polar diameter. Generalized linear mixed models

228 (GLMM) were used to assess interspecific differences in egg volume and fecundity (egg  
229 number), including species as factor, mother beetle as a random effect nested within  
230 species, and maternal lifetime (days) as covariate.

### 231 **Intraguild interaction trials**

232 We conducted a series of incubation trials to test the hypothesis that the outcome of  
233 the intraguild interaction among the larvae of *Pachymerus* and *Speciomerus* depends on  
234 the timing of infestation. In July 2013, we collected 257 ripe intact fruits directly from  
235 the canopy of five haphazardly selected palms along Pipeline road in SNP, using a pole  
236 pruner. The exo- and mesocarp of each fruit were completely removed with a knife, and  
237 fresh unhatched eggs (i.e. laid less than 24 hours before) of both species were placed  
238 onto the bare endocarps to create the following six experimental treatments: 1) one egg  
239 of *Pachymerus*; 2) one egg of *Speciomerus*; 3) one egg of each species simultaneously  
240 ('P0' hereafter); 4) one egg of each species with a 10 day head start for *Pachymerus*  
241 ('P10' hereafter); 5) one egg of each species with a 30 day head start for *Pachymerus*  
242 ('P30'); and 6) a control group without egg addition. The endocarps were incubated  
243 individually in transparent plastic cups with pierced lids to allow air movement, and  
244 adult emergences were monitored during the next wet season until they ceased. Each  
245 endocarp was then classified by three possible outcomes: emergence of a *Pachymerus*  
246 adult, a *Speciomerus* adult, or neither.

247 We used three contingency analyses to evaluate differences in beetle emergence  
248 patterns among egg addition treatments. The first compared the control, *Pachymerus*-  
249 only and *Speciomerus*-only treatments to assess the effectiveness of the egg addition  
250 treatments. This identified bruchid infestations prior to fruit collection (emergence from  
251 the control treatment) and the viability of the experimental eggs added to the endocarps.  
252 The second contingency analysis compared the *Pachymerus*-only, *Speciomerus*-only  
253 and P0 treatments to assess the impact of interspecific interaction between the two  
254 bruchid species. Significantly lower emergence of either species in the simultaneous  
255 infestation treatment compared to the appropriate single species treatment would  
256 indicate that the interspecific interaction is costly. The final contingency analysis  
257 compared the P0, P10, and P30 treatments to assess the effect of the timing of  
258 oviposition on the outcome of the interspecific interaction.

### 259 **Seed fates in the field**

260 We conducted a field study during July 2013 to quantify among-site differences in  
261 the relative abundance of the two bruchids and to determine whether this variation was  
262 correlated with differences in rodent abundance and associated levels of feeding on  
263 *Attalea* seeds. We investigated the fate of endocarps collected from the forest floor and  
264 top soil (5 cm depth). In BCI and SNP we selected six and five 50-m radius circular  
265 plots, respectively. The plots were separated by more than 250 m and located in  
266 secondary forests avoiding steep slopes and streams. In Gatun lake we selected 11 small  
267 (< 1.5 ha) islets known to be almost defaunated (see Adler & Seamon, 1991). At each  
268 plot/islet we collected all the endocarps under focal *Attalea* individuals (4-6 trees per  
269 plot in BCI and SNP, and 1-6 trees per islet upon availability). We defined the area

270 under a palm as the area within 3 m of the trunk (i.e.  $\sim 28 \text{ m}^2$ ). We avoided fruiting  
271 individuals in order to avoid collecting endocarps from the current season. All  
272 endocarps sampled were between 1 to 3 years old, so that any surviving beetle would  
273 already have emerged before the seeds were collected.

274 We examined the endocarps to determine the fates of their seeds (cf. Wright *et al.*  
275 2000, Visser *et al.* 2011). Emerging bruchids leave distinct circular exit holes that differ  
276 in diameter between *Speciomerus* ( $6.1 \pm 0.53 \text{ mm}$ ) and *Pachymerus* ( $4.9 \pm 0.54 \text{ mm}$ ,  
277 mean  $\pm$  SD,  $n = 16$  per species). The three rodent species leave different tooth marks:  
278 agoutis gnaw holes in the sides of the endocarp, red-tailed squirrels leave long gashed  
279 tooth marks and triangular openings at one end of the endocarp (Gálvez & Jansen  
280 2007), and spiny rats split the endocarps in half leaving a clean and polished cut (S.J.  
281 Wright, personal observation). Agoutis and squirrels make smaller openings when  
282 extracting bruchid larvae ( $38.1 \pm 17.5 \text{ mm}^2$ ,  $n = 12$ ) than when extracting seeds ( $116 \pm$   
283  $31.8 \text{ mm}^2$ ,  $n = 10$ , mean  $\pm$  SD; data from Gálvez & Jansen 2007), hence we could  
284 distinguish seed predation from larval predation (Visser *et al.* 2011).

285 Thus, all collected endocarps were classified into one of eight distinct seed fates:  
286 intact endocarp (I), endocarp opened by a spiny rat (R), endocarp opened by an agouti  
287 to extract a bruchid larva (Abr) or the seed (Asd), endocarp opened by a squirrel to  
288 extract a bruchid larva (Sbr) or the seed (Ssd), endocarp with a *Speciomerus* emergence  
289 hole (Spec), and endocarp with a *Pachymerus* emergence hole (Pach). We calculated the  
290 proportions of each seed fate for each focal tree. We also measured the maximum width  
291 and length for a representative sub-sample ( $\sim 50\%$ ) of the collected endocarps at each  
292 focal tree, and calculated their volume assuming equivalence with a prolate spheroid.

293 To quantify differences in seed fates among site types (protected BCI, hunted SNP  
294 and completely defaunated islets), we analyzed variation among focal trees in the  
295 proportions of endocarps in different categories. We used GLMMs with binomial errors  
296 and included plot/islet as a random effect. We performed five analyses:

- 297 1. To determine whether rodent activity paralleled the defaunation gradient, we  
298 analyzed the proportion of endocarps handled by rodents  $[(R + Abr + Asd + Sbr +$   
299  $Ssd)/\text{Total}]$ .
- 300 2. To determine how bruchid abundance varied over the defaunation gradient, we  
301 analyzed the proportion of endocarps with bruchid emergence  $[(\text{Spec} +$   
302  $\text{Pach})/\text{Total}]$ .
- 303 3. To determine how bruchid escape from agoutis and squirrels varied over the  
304 defaunation gradient, we analyzed the proportion of bruchid infested endocarps  
305 from which a bruchid emerged  $[(\text{Spec} + \text{Pach})/(\text{Spec} + \text{Pach} + \text{Abr} + \text{Sbr})]$ .
- 306 4. To determine how the relative abundance of the two bruchids varied over the  
307 defaunation gradient, we analyzed the proportion of bruchid emergences comprised  
308 by *Speciomerus*  $[\text{Spec}/(\text{Spec} + \text{Pach})]$
- 309 5. To evaluate potential consequences of defaunation-related variation in seed  
310 predation for *Attalea* population dynamics, we analyzed the proportion of intact  
311 endocarps that escaped bruchid and rodent attack  $[\text{I}/\text{Total}]$ .

312 According to previous research (Wright et al. 2000), across Central Panama the  
313 abundance of squirrels and agouties combined explains 68% of the variation in the  
314 abundance of vertebrates at a community level, so that their abundance can be  
315 considered a reliable proxy for the level of defaunation more generally (see Fig. S1 in  
316 Supporting Information). To further illuminate how the two bruchid species respond  
317 quantitatively to variation in rodent activity, we fit models for *Pachymerus* emergence  
318 [Pach/Total], *Speciomerus* emergence [Spec/Total], and *Speciomerus* relative  
319 abundance [Spec/(Spec+Pach)] as a function of the proportion of endocarps handled by  
320 rodents [(R+Abr+Asd+Sbr+Ssd)/Total]. We fit these three relationships using GLMMs  
321 or, if nonlinear generalized additive mixed models (GAMMs), with binomial error  
322 distributions and plot/islet as a random factor nested with site type (SNP, BCI or islets).

323 To test whether rodents prefer larvae to seeds, we investigated how the proportion of  
324 larvae predated by rodents [(Abr+Sbr)/(Abr+Sbr+Spec+Pach)] change with the  
325 proportion of seeds predated by rodents [(Asd+Ssd)/(Asd+Ssd+Intact)]. We fit a GAM  
326 for larval predation as a function of seed predation to quantify the relationship between  
327 the two. Because it is impossible to differentiate between larval and seed predation in  
328 the endocarps handled by rats, they were excluded from this analysis.

329 Finally, we assessed if the two bruchid species differ in the sizes of the endocarps  
330 they exploit. We conducted a GLMM on log-transformed endocarp volume, with site,  
331 emerging bruchid species and their interaction as fixed factors and plot/islet nested  
332 within site as a random effect. *P*-values were obtained by normal and Kenward-Roger  
333 approximation of degrees of freedom with pbkrtest (Halekoh & Højsgaard 2012).

334 All analyses were done with the R packages geepack (Højsgaard & Halekoh 2006),  
335 gamm4 (Wood 2011) and lme4 (Bates *et al.* 2014). Best models were selected  
336 according to AIC and model assumptions were validated graphically.

## 337 **Results**

### 338 **Reproductive ecology**

339 The two bruchid species differed in their emergence phenology, reproductive traits  
340 and oviposition preferences. Adults of *Pachymerus*, the smaller species, emerged  
341 significantly earlier in the fruiting season (interaction day\*species,  $Wald = 25.2$ ,  $P <$   
342  $0.0001$ ) than *Speciomerus*, although the emergence times overlapped substantially (see  
343 Fig. S2). Egg volume was almost 20 times larger in *Speciomerus* than in *Pachymerus*  
344 ( $F_{1, 406} = 10171$ ,  $P < 0.0001$ , Fig. 2a), whereas *Pachymerus* females laid 5 times more  
345 eggs than *Speciomerus* ( $F_{1, 31} = 8.2$ ,  $P < 0.01$ , Fig. 2b). Maternal lifetime did not affect  
346 fecundity ( $F_{1, 31} = 0.7$ ,  $P = 0.4$ ).

347 *Speciomerus* females overwhelmingly chose to attach their eggs to the endocarp, i.e.  
348 in areas where the flesh had been removed, whereas *Pachymerus* preferred the exocarp  
349 and specifically under the bracts ( $Z_{1, 29} = 8.9$ ,  $P < 0.0001$ , Fig. 2c). Consequently, given  
350 the choice of one fully de-fleshed, one partially de-fleshed, and one intact fruit as  
351 potential sites for egg deposition, *Speciomerus* females laid almost no eggs on intact  
352 fruits (just 1 of 241), and laid 2.4 times more eggs on fully de-fleshed than on partially

353 de-fleshed fruits, whereas *Pachymerus* laid almost no eggs on fully de-fleshed fruits  
354 (just 18 of 1676), and laid 1.5 times more eggs on intact than on partially de-fleshed  
355 fruits (Fig. 2d). Thus, the two species showed significant differences in the proportions  
356 of eggs laid on each fruit type (fully de-fleshed  $Z_{1,31} = 5.5$ ,  $P < 0.0001$ ; partially de-  
357 fleshed  $Z_{1,28} = -2.6$ ,  $P < 0.05$ ; intact:  $Z_{1,28} = -2.5$ ,  $P < 0.05$ ). Maternal lifetime did not  
358 affect the probability of laying an egg on an endocarp ( $Z_{1,30} = 0.7$ ,  $P = 0.5$ ).

### 359 **Intraguild interactions**

360 Patterns of beetle emergence differed significantly between egg addition treatments  
361 (Fig. 3a;  $\chi^2 = 44$ ,  $df = 10$ ,  $P < 0.0001$ ). *Pachymerus* adults emerged from 30% of the  
362 endocarps in the control group, which received no experimental egg addition, implying  
363 that this species infested seeds directly in the canopy, before fruit collection (Fig. 3a).  
364 Adding a *Speciomerus* egg increased emergence of *Speciomerus* adults from zero to  
365 25% ( $\chi^2 = 18.5$ ,  $df = 2$ ,  $P < 0.0001$ , Fig. S3b), whereas the increase of *Pachymerus*  
366 emergences in the *Pachymerus*-only treatment was not significant compared with those  
367 in the control group ( $\chi^2 = 2.2$ ,  $df = 2$ ,  $P = 0.14$ , Fig. S3a).

368 The reduction in the expected number of adult emergences in the P0 treatment (i.e.  
369 simultaneous egg addition of both species) compared with the *Pachymerus*-only ( $\chi^2 =$   
370  $11.6$ ,  $df = 2$ ,  $P < 0.01$ , Fig. S3c) and with the *Speciomerus*-only ( $\chi^2 = 7.6$ ,  $df = 2$ ,  $P <$   
371  $0.05$ , Fig. S3d) suggests that interspecific competition is costly for both species. When  
372 in direct competition for the same seed, the relative success of the two species depended  
373 on the relative timing of egg addition ( $\chi^2 = 10.3$ ,  $df = 4$ ,  $P < 0.05$ , Fig. 3b). When  
374 *Pachymerus* was given a head start of 30 days, there was no emergence whatsoever of  
375 *Speciomerus*, compared with 42% for *Pachymerus*. In contrast, when both eggs were  
376 added at the same time or when *Pachymerus* had a head start of just 10 days,  
377 *Speciomerus* emerged from 14-15% of all endocarps, whereas *Pachymerus* emerged at  
378 rates similar to the control.

### 379 **Seed fate in the field**

380 6569 *Attalea* endocarps were collected from beneath 84 focal palms (BCI: mean  
381  $67 \pm 12$  SE endocarps per palm; SNP:  $70 \pm 13$ ; islets:  $100 \pm 20$ ). At each site, around a third  
382 of the recovered endocarps were intact (Fig. 4a). The frequency with which seeds were  
383 attacked by rodents varied strongly between the three site types as predicted (Fig. 4a:  
384  $Z_{\text{SNP}} = -4.5$ ,  $P < 0.0001$ ,  $Z_{\text{Islets}} = -2.8$ ,  $P < 0.001$ , contrasts relative to BCI which was  
385 the intercept level of the models, see Table S1 for parameter estimates). In BCI, 64.7%  
386 of the endocarps were opened by rodents, compared with 17.7% in SNP and 11.6% in  
387 the islets. In BCI and SNP the most abundant rodent scars were from agoutis and  
388 squirrels, whereas on the islets most scars were made by spiny rats (Fig. 4b).

389 The proportion of seeds from which bruchids emerged showed the opposite pattern  
390 of variation among site types (Fig. 4a:  $Z_{\text{SNP}} = 4.8$ ,  $P < 0.0001$ ,  $Z_{\text{Islets}} = 4.4$ ,  $P < 0.0001$ ):  
391 just 6.3% of seeds on BCI had bruchid emergence holes, compared to more than half of  
392 endocarps in SNP and the islets. The proportion of bruchid infestations that resulted in  
393 adult emergences was lower on BCI than SNP and the islets ( $Z_{\text{SNP}} = 3.4$ ,  $P < 0.0001$ ,

394  $Z_{\text{Islets}} = 6.7, P < 0.0001$ ), reflecting higher levels of larval predation by rodents on BCI  
395 (Fig. 4c). There was a significant difference between sites in the relative abundance of  
396 the two bruchid species (Fig. 4d:  $Z_{\text{SNP}} = -6.7, P < 0.001, Z_{\text{Islets}} = -7.9, P < 0.001$ ).  
397 *Speciomerus* was overwhelmingly dominant on BCI, accounting for 95% of bruchid  
398 emergences whereas *Pachymerus* dominated on the islets with 70 % of the emergences,  
399 and the two species had similar abundances at SNP (Fig. 4d).

400 Variation in rodent attack among focal trees was strongly and differentially related to  
401 variation in the success of the two bruchid species (Fig.5). The emergence of  
402 *Pachymerus* decreased as the levels of rodent attack increased ( $Z_{1,84} = -14.2, P <$   
403  $0.0001$ , Fig.5a). In contrast, *Speciomerus* emergences peaked at intermediate levels of  
404 rodent attack ( $\chi^2 = 66.1$ , estimated  $df = 4.2, P < 0.0001, r^2 = 0.35$ , Fig.5b) and its  
405 relative abundance reached almost total dominance when rodents were abundant ( $Z_{1,84}$   
406  $= 15.2, P < 0.0001$ , Fig.5c). Larval predation risk was higher than rodent seed predation  
407 risk at the vast majority of focal trees, with the fitted relationship far above the 1:1 line  
408 for most of the range of the data (estimated  $df = 4.6; F = 50.3; P = 0.0001, r^2 = 0.78$ ,  
409 Fig. S4).

410 Measurements of endocarp size in 1728 endocarps provided no clear indication of  
411 differences in endocarp-size preferences between the bruchids (Table S2 and Fig. S5).  
412 *Speciomerus* emerged from slightly larger endocarps than *Pachymerus* in BCI ( $8.4 \pm$   
413  $0.2$  versus  $6.5 \pm 0.6$  respectively; mean  $\pm 1$  SE in  $\text{cm}^3$ ) and the islets ( $6.9 \pm 0.1$  and  $6.6$   
414  $\pm 0.06$ ), but there were no differences in PLR ( $8.1 \pm 0.1$  versus  $8.2 \pm 0.1$ ).

## 415 Discussion

416 We investigated how vertebrates affected competitive interactions between two  
417 specialized seed predators of the palm *Attalea butyracea*. We found that the larger  
418 bruchid *Speciomerus* was the superior competitor in direct competition for a given seed  
419 but required the removal of the exo- and mesocarp of the fruits by a vertebrate frugivore  
420 before oviposition. The smaller but more fecund *Pachymerus* infested seeds inside  
421 intact fruits directly in the canopy, gaining a head start on its post-dispersal competitor.  
422 *Pachymerus* emergence dominated in the defaunated sites, but its dominance decreased  
423 as the proportion of seeds attacked by rodents increased. Rodent abundance is well  
424 correlated with the abundances of other mammals and serves as proxy for defaunation  
425 (Fig. S1). These results provide evidence for vertebrates influencing competitive  
426 interactions between seed predators, as well as for cascading effects of defaunation on  
427 species coexistence.

## 428 Niche differentiation

429 The two bruchids showed pronounced differences in their reproductive ecology. The  
430 differences in egg volume and fecundity are consistent with a classical evolutionary  
431 trade-off between offspring size and number (Smith & Fretwell 1974). The finding that  
432 *Pachymerus* females preferred to oviposit on intact fruits along with the observation  
433 that incubated seeds collected directly from palms and subsequently stripped of exo-  
434 and mesocarp frequently already contained *Pachymerus* larvae indicates that this

435 species oviposits on infructescences in the canopy. The same pre-dispersal oviposition  
436 behavior has been observed in the congener *P. bactris*, which infests seeds of the palm  
437 *Astrocaryum standleyanum* (Jansen *et al.* 2010). *Speciomerus* females, in contrast,  
438 exclusively laid their eggs on defleshed or partially defleshed endocarps that are  
439 typically available below parent palms (Wilson & Janzen 1972; Wright 1983). Several  
440 rodents cache these endocarps as food supplies out of reach of *Speciomerus* (Jansen *et*  
441 *al.* 2010, 2012, 2014), shortening the temporal window to lay their eggs. This, along  
442 with the uncertainty about prior infestation by its pre-dispersal competitor may have  
443 favored greater larval competitive ability and the almost 20 fold larger energy  
444 investment per egg.

445 This interpretation of a more opportunistic versus a more conservative reproductive  
446 strategy fits with bet-hedging theory predictions on optimal progeny size (Fox &  
447 Czesak 2000). A harsh environment (e.g. low-density of oviposition sites and highly  
448 variable seed quality) is expected to select for adaptations that increase offspring  
449 survival such as larger egg sizes at the cost of lower fecundity (Czesak & Fox 2003),  
450 whereas an abundance of aggregated oviposition sites should select for a lower parental  
451 investment per egg and greater fecundities (Fox & Czesak 2000).

452 *Pachymerus* emerges earlier than *Speciomerus* at the onset of the wet season (Fig.  
453 S2), consistent with its pre-dispersal oviposition behavior. However, the substantial  
454 overlap in adult activity of the two bruchid species precludes a resource partitioning  
455 based on phenological differences (Espelta *et al.* 2009). The larvae of *Attalea* seed  
456 predators exhibited intraguild predation, with only one adult emerging per seed despite  
457 multiple infestations, consistent with previous observations (Wilson & Janzen 1972;  
458 Wright 1983). The incubation trials demonstrated that the outcome of this larval  
459 predation depends on the duration of the head start of the pre-dispersal seed parasitoid  
460 versus its post-dispersal competitor. Similar results have been found with the bruchid  
461 *Callosobruchus maculatus* in which just two days of head start allowed the larvae of a  
462 less competitive strain to equal its more aggressive competitor (Messina 1991). These  
463 results highlight that oviposition strategy, i.e., seed infestation before or after primary  
464 dispersal, is a main axis of niche divergence for insect seed predators and is associated  
465 with several other life history traits, such as adult phenology, egg size/number and  
466 oviposition preferences (Messina 1991; Traveset 1991; Johnson & Romero 2004).

## 467 **Cascading effects of defaunation**

468 Our study sites represented a sharp defaunation gradient (Adler and Seamons 1991,  
469 Wright *et al.* 2000), as shown by striking differences in the proportion of endocarps  
470 handled by rodents. Bruchid emergence relative to bruchid infestation was much higher  
471 in defaunated sites, probably due to the lower rates of larval predation by rodents.  
472 Rodents preferentially prey upon bruchid larvae (Fig. S4) in accordance with previous  
473 studies suggesting that rodents can exert a strong top-down control over insect  
474 populations (Wright & Duber 2001; Gálvez & Jansen 2007; Visser *et al.* 2011). This  
475 top-down pressure had differential effects on the two competing seed predators. The  
476 relative abundance of *Speciomerus* increased with the levels of rodent attack, with

477 *Speciomerus* being almost absolutely dominant on Barro Colorado where the level of  
478 larval predation by rodents was highest, while *Pachymerus* dominated at the most  
479 defaunated sites. One plausible reason is that *Speciomerus* is favored by the higher  
480 abundance of vertebrate frugivores which expose endocarps as soon as fruits are ripe,  
481 thus reducing the headstart of *Pachymerus*. In addition to rodents, many other vertebrate  
482 species feed upon *Attalea* fruits and there are remarkable differences in frugivory rates  
483 across central Panama linked with defaunation levels (Wright et al. 2000). Therefore,  
484 vertebrate frugivores and granivores may play a dual mutualistic and antagonistic role  
485 and modify the outcome of the intraguild predation of bruchids competing for *Attalea*  
486 seeds even at rather local scales (Fig. 5). If so, natural variation in vertebrate abundance  
487 and consumption of *Attalea* fruits at a landscape level would ultimately enable the  
488 coexistence of both bruchid species. A similar mechanism has been hypothesized to  
489 facilitate coexistence of specialized host-sharing milkweed aphids via spatial variation  
490 in the abundance of ants that promote their tended species by suppressing their superior  
491 non-tended competitors (Smith et al. 2008).

## 492 **Conclusions**

493 Natural food webs are spatially dynamic but empirical field-based evidence of how  
494 spatial variation in multi-trophic interactions affects species coexistence are scant  
495 (Amarasekare 2008). Vertebrates such as reptiles, birds and mammals are keystone  
496 ecological agents known to exert top-down control on the populations of insects at  
497 lower trophic levels (Böhm et al. 2011; Visser et al. 2011), and whose disappearance  
498 thus has cascade effects reverberating through entire food webs (Terborgh et al. 2001).  
499 Our results show that vertebrates may also modify the competitive balance of  
500 phytophagous insects sharing the same key resource, and can determine their relative  
501 abundances. Given the unprecedented rates of defaunation globally (Dirzo et al. 2014),  
502 this insight warns of potential unanticipated effects on biodiversity loss in hyperdiverse  
503 groups such as phytophagous insects.

## 504 **Acknowledgements**

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509 Perez, Chelina Batista and Gustavo Bornemann for assistance with field work.

## 510 **Data Accessibility**

511 Data available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.gc850>  
512 (Peguero et al. 2016).

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## 618 **Supporting Information**

619 Additional Supporting Information may be found in the online version of this article.

620 **Figure S1.** Correlation between rodent and vertebrate abundance across central Panama.

621 **Figure S2.** Phenology of *Pachymerus* and *Speciomerus* adult emergence.

622 **Figure S3.** Association plots of egg incubation trials.

623 **Figure S4.** Relationship between larval predation and seed predation by rodents.

624 **Figure S5.** Variation in *Attalea* endocarp volume by insect species and across sites.

625 **Table S1.** Results of the analyses on *Attalea* seed fate differences across sites.

626 **Table S2.** Results of the analysis of *Attalea* variance in endocarp volume.

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## 635 **Figures**

636 **Fig. 1.** Food web associated with the fruits and seeds of the palm *Attalea butyracea* in  
637 Central Panama. Numbers denote different trophic interactions: 1. Fruit pulp feeding; 2.  
638 Seed feeding; 3. Predation of bruchid larvae by rodents; 4. Intraguild predation of  
639 larvae. Defaunation cascades down the web to affect the fate of the palm seeds.

640 **Fig. 2.** Differences between the *Attalea* seed predators *Pachymerus cardo* and  
641 *Speciomerus giganteus* in egg size (a), egg number (b), and oviposition preferences in  
642 terms of preferred fruit tissue (c) and level of endocarp defleshing (d). Central lines are  
643 medians, boxes are 1<sup>st</sup> and 3<sup>rd</sup> quartile and whiskers show min and max values. Note

644 log-scale in panels a and b. Overlaid numbers in panels c and d show the number of  
645 eggs. Significance levels (from GLMMs) are \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; and \*\*\*  $P < 0.001$ .

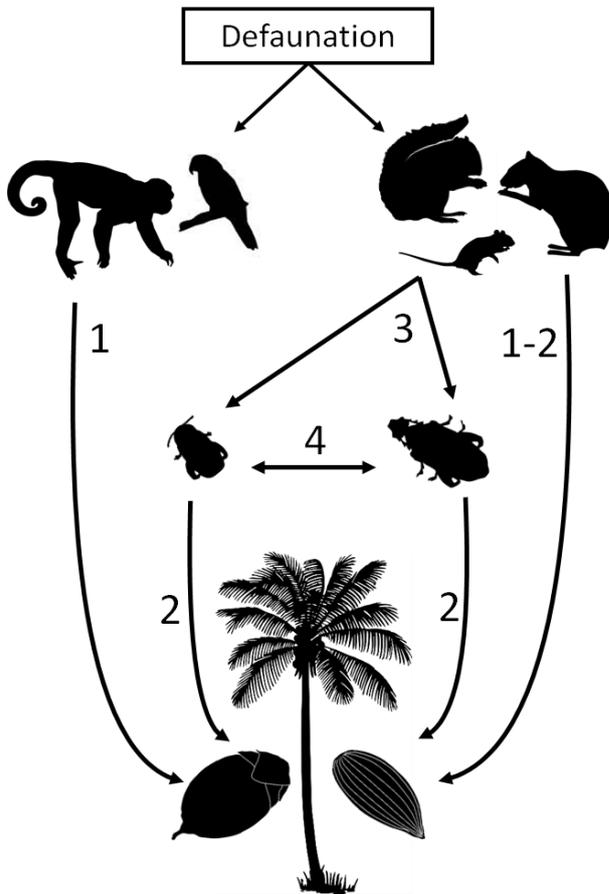
646 **Fig. 3.** Results of the trials in which *Attalea* seeds were incubated with and without  
647 addition of eggs of one or both species of the bruchid seed parasitoids *Pachymerus* and  
648 *Speciomerus*. Treatments were a control group of fruits directly collected from palms  
649 incubated without egg addition, and experimental additions of eggs of *Pachymerus*  
650 only, of both species with a head start of 0, 10 or 30 days for *Pachymerus* (P0, P10 and  
651 P30, respectively), and of *Speciomerus* only. (a) Differences among treatments in  
652 bruchid emergence. Overlaid numbers show counts for each outcome. (b) Association  
653 plot for the contingency analysis of treatments P0, P10 and P30 ( $\chi^2 = 10.3$ ,  $df = 4$ ,  $P <$   
654  $0.05$ ). Numbers above and below the bars show the frequencies of each outcome for  
655 each treatment. The height of the bars is proportional to the corresponding Pearson  
656 residual. Within each treatment, the width of the bars is proportional to the frequency of  
657 the outcome (with frequency 0 assigned an arbitrary width). The significance level is for  
658 the overall analysis with pink indicating the strongest deviation from the null hypothesis  
659 of independence between treatments and outcomes.

660 **Fig. 4.** Fates of *Attalea* seeds collected from sites with different levels of defaunation in  
661 Central Panama. (a) Proportion of seeds with a bruchid emergence hole, opened by  
662 rodents, and intact. (b) Proportion of seeds opened by squirrels, agouties or spiny rats  
663 relative to all seeds handled by rodents; (c) Proportion of seeds with signs of larval  
664 predation by a rodent and with a bruchid emergence hole relative to all bruchid-infested  
665 seeds; (d) Proportion of endocarps with bruchid emergence holes classified by bruchid  
666 species. Overlaid numbers show counts for each seed fate. Associated p-values are  
667 given in the text.

668 **Fig. 5.** Relationship of bruchid emergence with the frequency of rodent attack on seeds  
669 along a defaunation gradient in Central Panama. Percentages of (a) *Pachymerus*  
670 emergence relative to all seeds [Pach/Total]; (b) *Speciomerus* emergences relative to all  
671 seeds [Spec/Total]; and (c) *Speciomerus* emergences relative to all bruchid emergences  
672 [Spec/(Pach+Spec)]. Rodent attack is defined by the proportion of seeds opened by  
673 rodents [(Sbr + Ssd + Abr + Asd + R)/Total]. Solid lines show regression fits according  
674 to generalized linear (a, c) or additive (b) mixed models with binomial errors and with  
675 plot nested within site as a random factor. Dotted lines show 95% confidence envelopes.  
676 Each point corresponds to a single focal tree, with point size proportional to sample size  
677 (number of seeds) and colors indicating sampling site types (BCI = black, SNP = grey,  
678 and Islets = light grey).

679

680 **FIGURE 1**



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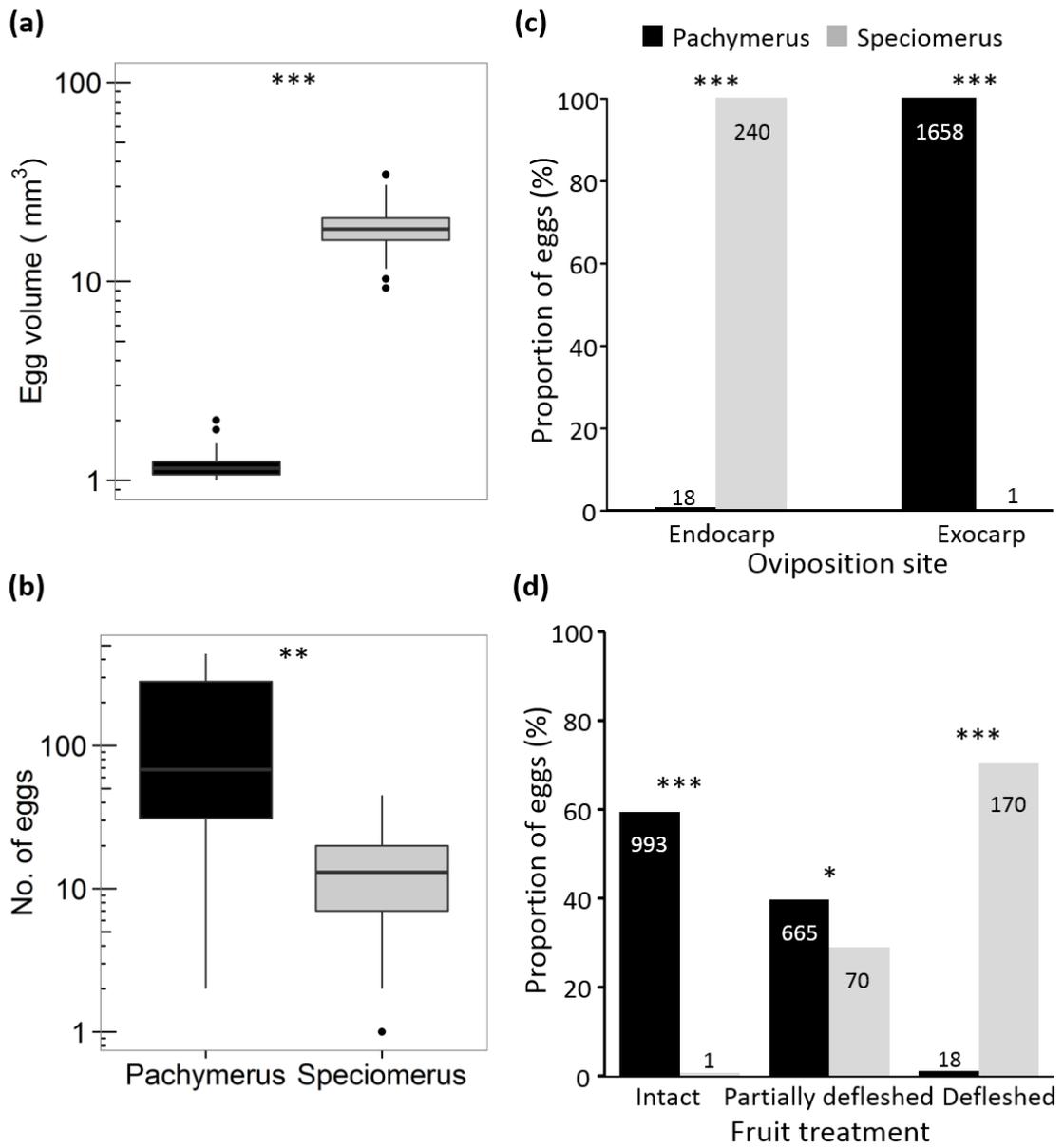
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695 FIGURE 2



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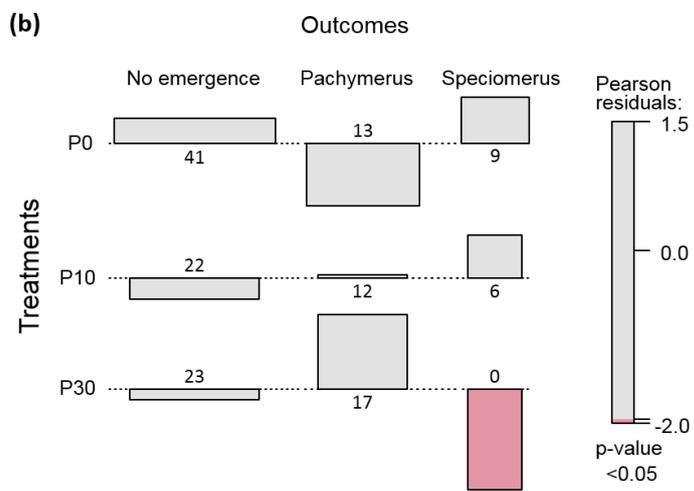
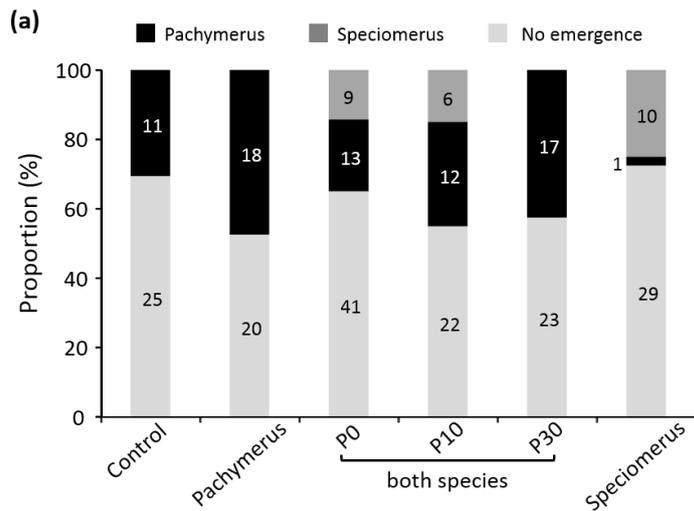
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705 **FIGURE 3**



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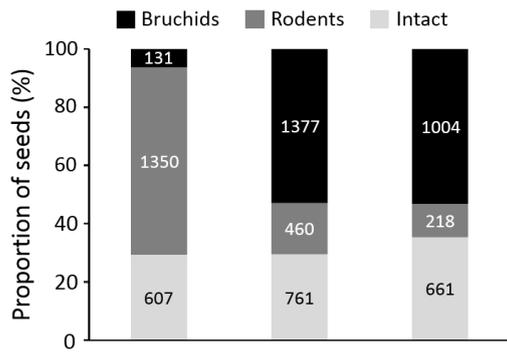
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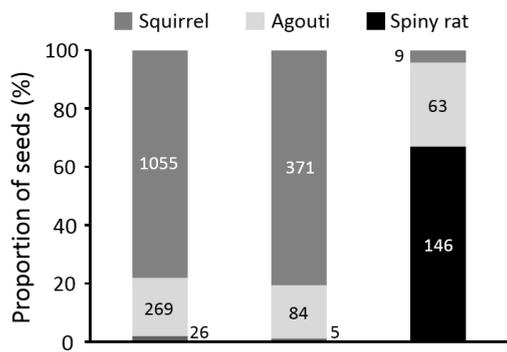
715

716 FIGURE 4

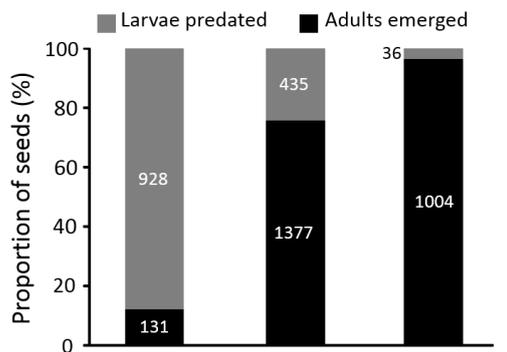
**(a) All endocarps**



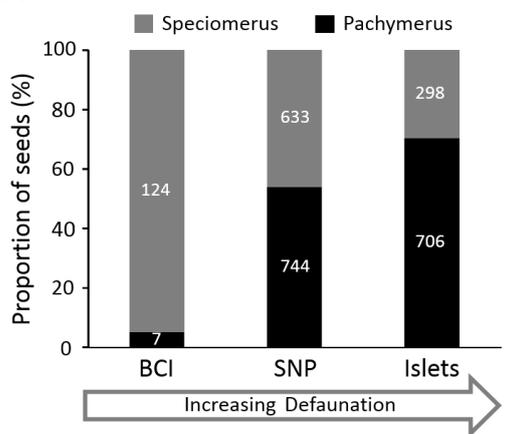
**(b) Handled by rodents**



**(c) Infested by bruchids**



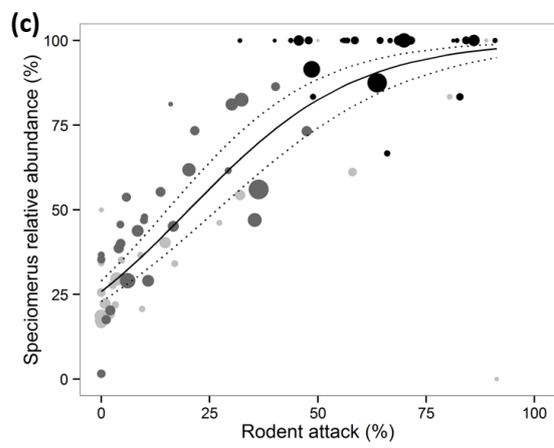
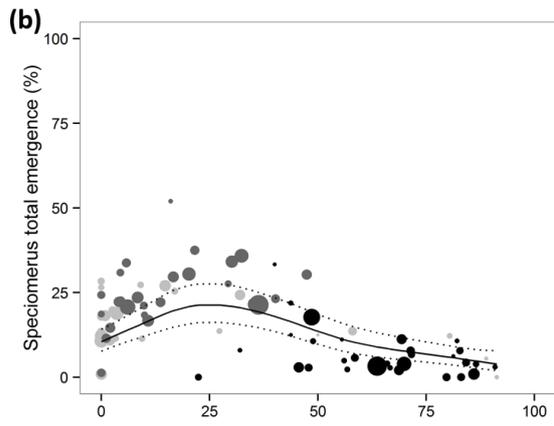
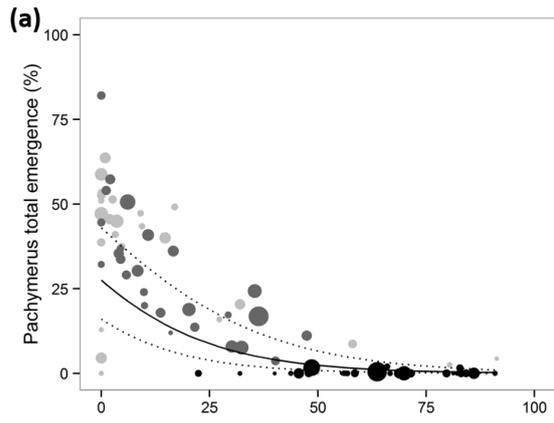
**(d) Bruchid emergences**



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719 **FIGURE 5**



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