

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 ± 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. ~28 m²). 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 ± 0.53 mm) and *Pachymerus* (4.9 ± 0.54 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 ± 17.5 mm², n = 12) than when extracting seeds ($116 \pm$
283 31.8 mm², 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 (~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)/Total].
- 300 2. To determine how bruchid abundance varied over the defaunation gradient, we
301 analyzed the proportion of endocarps with bruchid emergence [(Spec +
302 Pach)/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 [(Spec + Pach)/(Spec + Pach + Abr + 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* [Spec/(Spec+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 [I/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 ± 12 SE endocarps per palm; SNP: 70 ± 13 ; islets: 100 ± 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 respective 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 ± 0.6 respectively; mean ± 1 SE in cm^3) and the islets (6.9 ± 0.1 and 6.6
414 ± 0.06), but there were no differences in PLR (8.1 ± 0.1 versus 8.2 ± 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.

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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 1st and 3rd 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 *** $P < 0.001$.

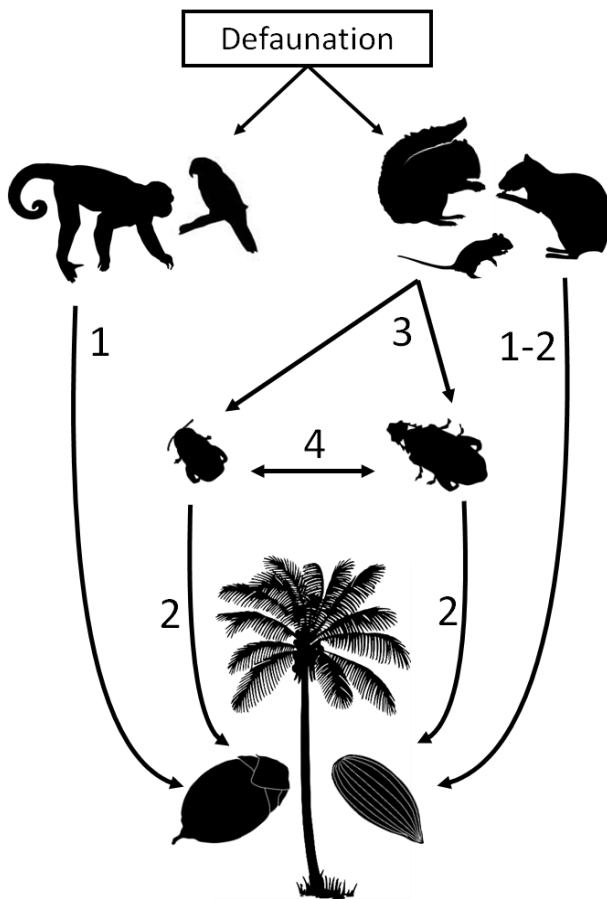
646 **Fig. 3.** Results of the trials in which *Attalea* seeds were incubated with and without
647 addition of eggs of one or both species of the bruchid seed parasitoids *Pachymerus* and
648 *Speciomerus*. Treatments were a control group of fruits directly collected from palms
649 incubated without 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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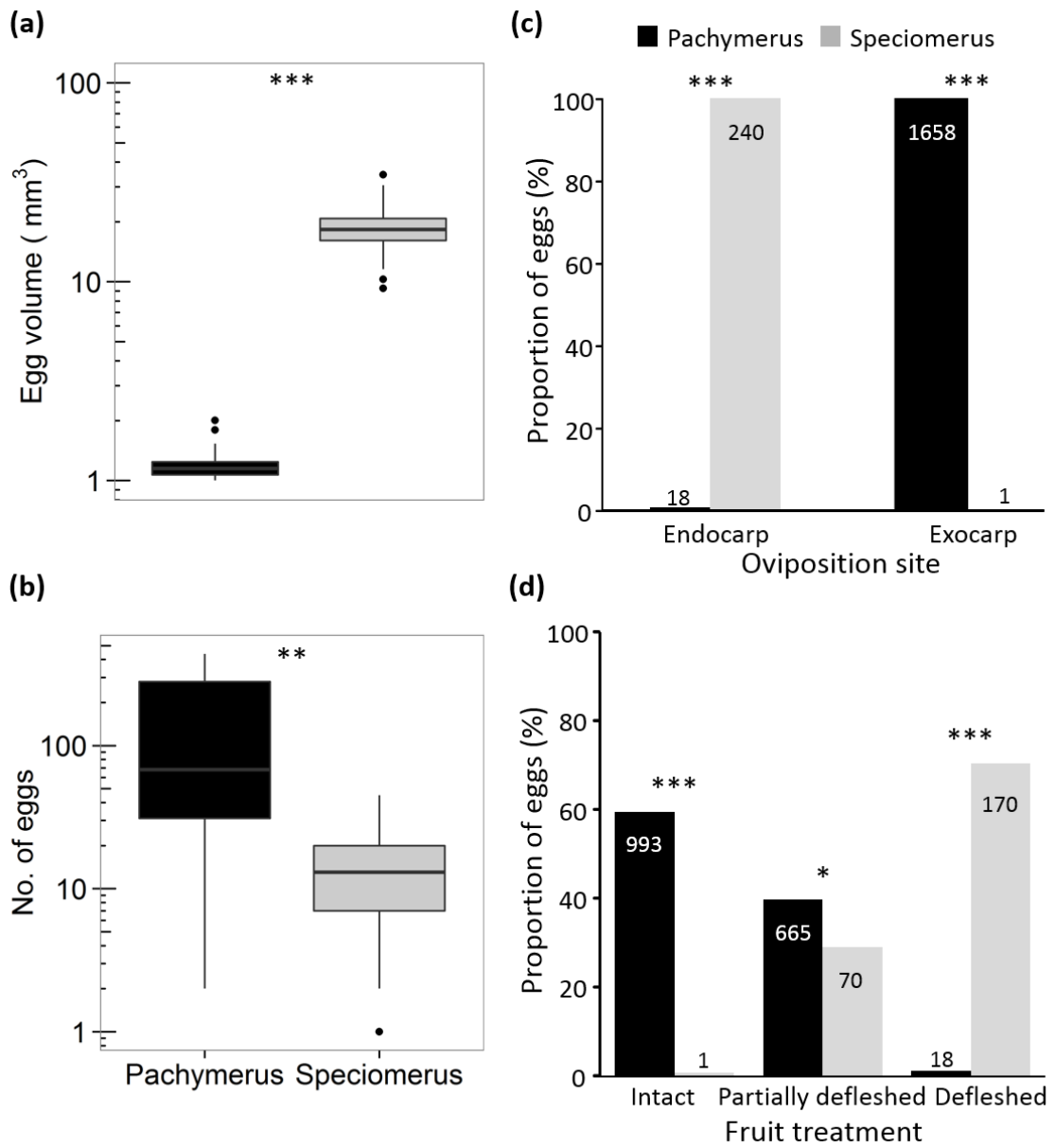
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695 FIGURE 2



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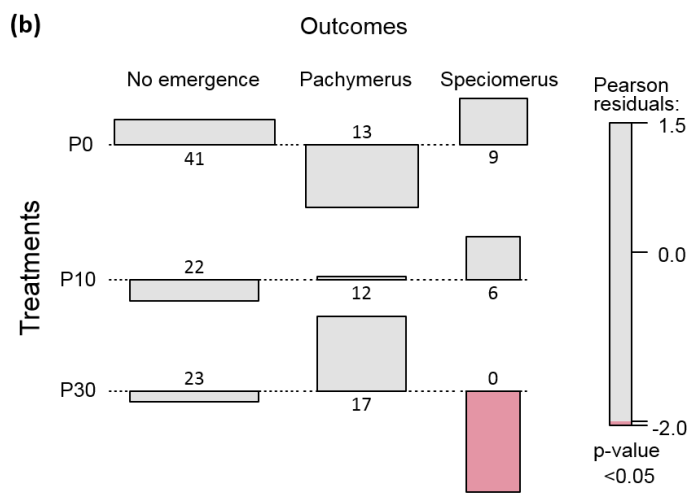
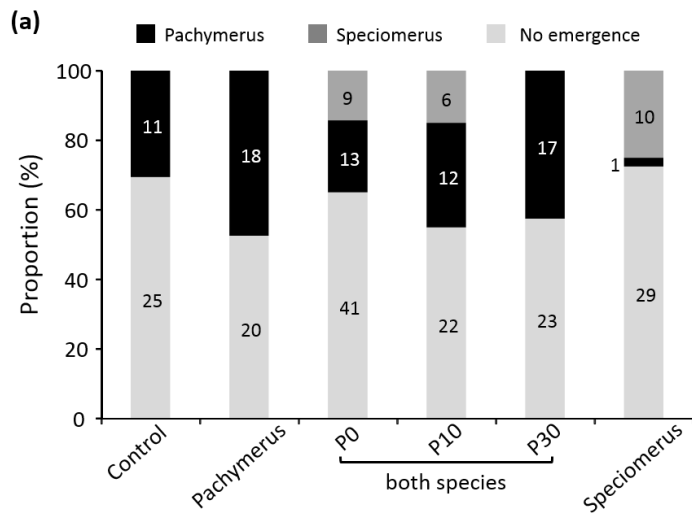
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705 **FIGURE 3**



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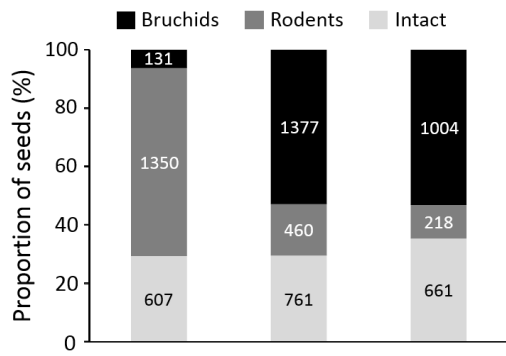
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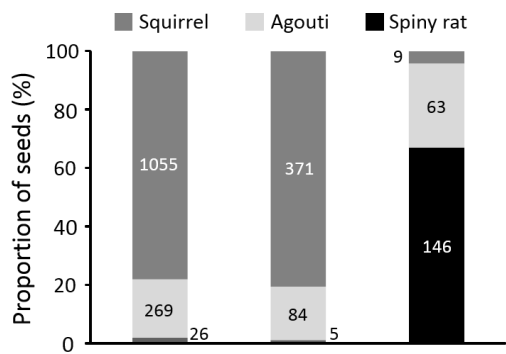
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716 **FIGURE 4**

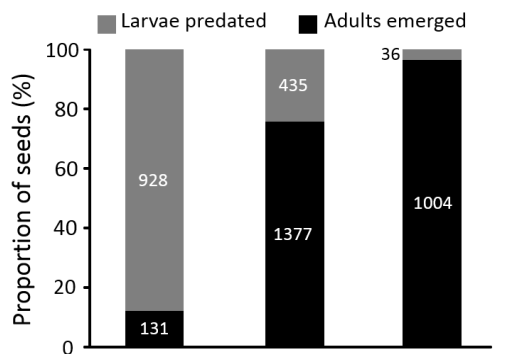
(a) All endocarps



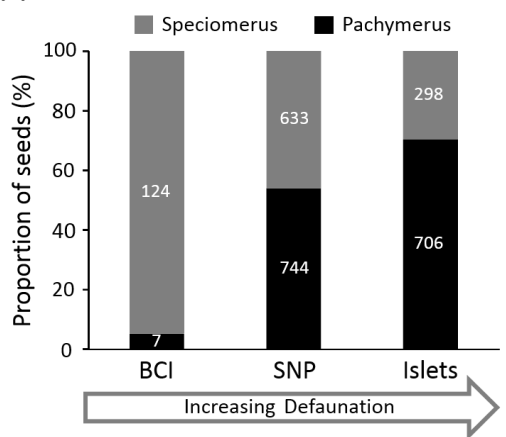
(b) Handled by rodents



(c) Infested by bruchids



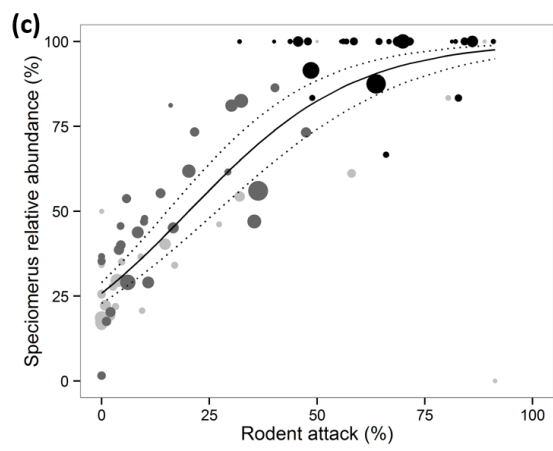
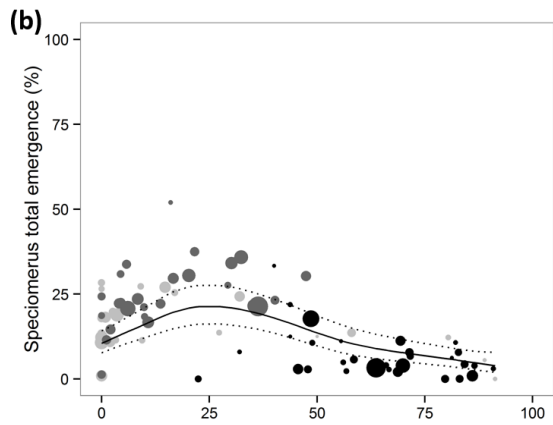
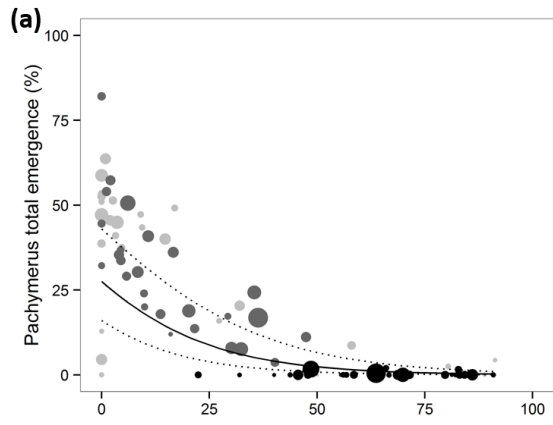
(d) Bruchid emergences



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719 **FIGURE 5**



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