

2014

Are Exotic Herbivores Better Competitors? A Meta-Analysis

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Citation/Publisher Attribution

Radville, L., Gonda-King, L., Gomez, S., Kaplan, I., & Preisser, E. L. (2014). Are exotic herbivores better competitors? A meta-analysis. *Ecology*, 95(1), 30-36. <http://dx.doi.org/10.1890/13-0728.1>

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ARE EXOTIC HERBIVORES BETTER COMPETITORS? A META-ANALYSIS

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24 **ABSTRACT:**

25 Competition plays an important role in structuring the community dynamics of
26 phytophagous insects. As the number and impact of biological invasions increase, it has become
27 increasingly important to determine whether competitive differences exist between native and
28 exotic insects. We used meta-analysis to test the hypothesis that native/exotic status affects the
29 outcome of herbivore competition. Specifically, we used data from 161 published studies to
30 assess plant-mediated competition in phytophagous insects. For each pair of competing
31 herbivores, we determined the native range and coevolutionary history of each herbivore and
32 host plant. Plant-mediated competition occurred frequently, but neither native nor exotic insects
33 were consistently better competitors. Spatial separation reduced competition in native insects but
34 showed little effect on exotics. Temporal separation negatively impacted native insects but did
35 not affect competition in exotics. Insects that coevolved with their host plant were more affected
36 by interspecific competition than herbivores that lacked a coevolutionary history. Insects that
37 have not coevolved with their host plant may be at a competitive advantage if they overcome
38 plant defenses. As native/exotic status does not consistently predict outcomes of competitive
39 interactions, plant-insect coevolutionary history should be considered in studies of competition.

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41 **KEYWORDS:** Interspecific competition, exotic herbivore, invasive species, meta-analysis,
42 plant-mediated competition, coevolutionary history, resource partitioning, plant defense

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46 **INTRODUCTION**

47 Interspecific competition structures phytophagous insect assemblages (Denno et al. 1995,
48 Reitz and Trumble 2002, Kaplan and Denno 2007) and can play an important role in the
49 establishment, success, and impact of exotic insects. In light of the growing number and impact
50 of exotic species, it is important to understand whether exotic status *per se* affects interspecific
51 competition between herbivorous insects.

52 There are several ways in which an herbivore's native or exotic status might affect the
53 outcome of interspecific competition. Exotic species are predicted to have a competitive
54 advantage over native species in interspecific interactions (Sakai et al. 2001). This may result
55 from reduced pressure from natural enemies, a factor known to contribute to the increased
56 competitive ability of some exotic insects (Connell 1970, Lawton and Brown 1986, Hanks and
57 Denno 1993). Exotics may also gain a competitive advantage if they are able to alter plant
58 quality or overcome plant defenses (Gandhi and Herms 2010, Prior and Hellmann 2010). For
59 example, Prior and Hellman (2010) suggest that the exotic gall-forming wasp *Neuroterus*
60 *saltatorius* negatively impacts a native butterfly, *Erynnis propertius*, via changes in nutritional
61 quality of the shared host plant. More generally, interactions between native and exotic
62 herbivores could be driven by the host plant in the context of evolutionary history. An exotic
63 species that lacks a coevolutionary history with their host plant may have a competitive
64 advantage because the plant has not evolved effective responses against it.

65 While there are a number of reasons to suspect that exotic species are generally strong
66 interspecific competitors, many examples suggest otherwise. Specifically, the failure of many
67 exotic species to establish and reach high densities may be linked to the competitive dominance
68 of native species. For example, Paini et al. (2008) suggested that the exotic thrips *Frankliniella*
69 *tritici* cannot reach high densities on the east coast of the United States because it is

70 competitively inferior to the native thrips *F. occidentalis*. More generally, exotic species may be
71 at a competitive disadvantage whenever they are maladapted to the novel ecosystem (Ward-Fear
72 et al. 2009). Despite the large number of studies addressing interspecific herbivore competition
73 for a given pair of species, we lack an overarching sense of whether a species' native/exotic
74 status and coevolutionary history with its host plant affects the outcome of interspecific
75 herbivore competition. We distinguish between these two factors since they are not necessarily
76 correlated; an exotic insect can, for instance, feed on its native host plant outside of both species'
77 native range (something that can occur when the host plant is itself exotic).

78 It is also possible that competing native and exotic species may respond differently to
79 spatial and temporal separation. Generally, spatiotemporal co-occurrence increases competition
80 due to a lack of niche partitioning (Schoener 1974). In support of this, Denno et al. (1995)
81 suggested that resource partitioning reduces, but does not eliminate, competition. If exotic
82 insects are less affected by induced plant defenses than their native competitors (Gandhi and
83 Herms 2010), the exotic species may not respond as strongly to co-occurrence and may be less
84 affected by the prior settlement or close proximity of a competitor.

85 We present the results of a meta-analysis assessing whether native/exotic status,
86 consumer-host coevolutionary history, and spatiotemporal co-occurrence affect the strength of
87 exploitative competition between herbivorous insects. Such competitive interactions can be
88 thought of as plant-mediated, since they occur when one phytophagous insect indirectly affects
89 another species through the first species' impact on the nutritional and/or chemical content of the
90 plant. We build on an exhaustive database of interactions between insect herbivores compiled by
91 Kaplan and Denno (2007); our restriction to plant-mediated interactions excludes apparent
92 competition and other enemy-mediated interactions from our analysis. The importance of

93 competition to phytophages has been established (Denno et al. 1995); rather than revisit this
94 question, we take a quantitative approach to address the importance of species invasions and
95 evolutionary history to the strength of competition. Our analysis also included two other factors,
96 spatial and temporal separation, known to affect the strength of competition. We examined these
97 issues by addressing the following four questions: (1) Do native and exotic herbivores respond
98 differently to interspecific competition; (2) Does the outcome of competition differ if the host
99 plant and herbivore share a coevolutionary history (i.e., whether or not they co-occur in their
100 native range); (3) Does native/exotic status alter the impact of spatial separation on interspecific
101 herbivore competition; and (4) Does native/exotic status alter the impact of temporal separation
102 on interspecific herbivore competition.

103 **METHODS**

104 **Identification and selection of studies:** Publications that assess interspecific competition
105 in phytophagous insects were located in several ways. Briefly, we updated the database analyzed
106 by Kaplan and Denno (2007) using the same search criteria. This database provides an
107 exhaustive survey of literature published before 2007; we added studies published between 2007
108 and 2011, as well as any prior studies inadvertently excluded from the 2007 database (see
109 Appendix for details determining study criteria).

110 In order to parallel the methods used in Denno et al. (1995) and Kaplan and Denno
111 (2007), we limited our database to studies evaluating interspecific competition between
112 phytophagous insects. In order to be included in the database, studies had to report the results of
113 plant-mediated interactions in terrestrial systems and assess one or more of the following
114 herbivore variables: growth, development time, fecundity, or survival. We chose these response
115 variables because they are commonly reported in the literature and have been used in previous

116 meta-analyses of plant-herbivore systems (Koricheva et al. 1998, Kaplan and Denno 2007). Each
117 paper had to report mean values for both control (defined as the focal insect's response in the
118 absence of a potential competitor) and experimental (defined as the focal insect's response in the
119 presence of a potential competitor) treatments, some measurement of variation around the mean,
120 and data on within-treatment sample size. Publications from the Kaplan and Denno (2007) meta-
121 analysis that did not meet these criteria were excluded from our analysis.

122 **Data collection:** From each relevant paper, we collected information about both the focal
123 herbivore (the species on which the response was measured) and the competing herbivore (the
124 species sharing the host plant with the focal herbivore in the experimental treatment). We
125 classified each herbivore according to its feeding location (leaf, stem, root, flower, fruit) and
126 whether the two herbivores were spatially or temporally separated (see Appendix). We also
127 classified each herbivore as native or exotic relative to where the study occurred; we considered
128 species as exotic when they were studied in a location outside of their native range. Finally, we
129 recorded whether the native range of the focal herbivore and host plant coincided in order to
130 determine whether the focal herbivore and host plant share a co-evolutionary history.

131 For each observation, i.e., the measurement of a single response variable on an
132 independent data point, we calculated a corresponding log response ratio (RR). The RR measures
133 the ratio of the response in the experimental group to the response in the control group. The log
134 response ratio is less than one if the measurement in the experimental treatment is less than in the
135 control treatment, and greater than one if the measurement in the experimental is greater than in
136 the control. Response variables were growth, fecundity, survival, and development time.
137 Increases in the first three variables were considered to be beneficial to the focal insect; in the
138 case of development time, however, an increase is generally considered to be harmful

139 (Haggstrom and Larsson 1995). In order to standardize the variables so that an increase was
140 always good for the insect, we multiplied the effect size values for development time by -1 so
141 that decreased development times are denoted by effect sizes greater than one (i.e., generally
142 beneficial to the herbivore) and increased development times are denoted by effect sizes less than
143 one (i.e., generally harmful to the herbivore).

144 **Statistical analysis:** MetaWin 2.0 (Rosenberg et al. 2000) was used to run all analyses
145 and compare mean effect sizes between groups. Random effects models for categorical data were
146 used to examine whether a series of predictor variables explained a significant amount of
147 variation in effect sizes. The predictor variables (native/exotic status, host plant/focal insect
148 coevolutionary history, degree of spatial separation, and degree of temporal separation) were
149 treated as random categorical variables.

150 The following comparisons were selected a priori: (1) focal herbivore is native/exotic
151 regardless of competing herbivore status; (2) host plant and focal insect do/do not co-occur in
152 their native range; (3) competing insects are/are not spatially separated; and (4) competing
153 insects are/are not temporally separated. Comparisons (3) and (4) were analyzed for differences
154 between native and exotic insects. Due to a lack of replication, we could not analyze (3) and (4)
155 for differences between coevolved and non-coevolved host and insect pairs. The mean effect size
156 and 95% confidence intervals for each predictor variable were used to evaluate the magnitude
157 and direction of the variable's impact on competitive outcomes. (See Appendix for more
158 methodological details.)

159 We analyzed comparisons 1-4 using both our full data set and a conservative
160 ('truncated') data set that uses one randomly-selected observation for each pair of competing
161 species per response variable. Because these two data sets only specify the native/exotic status of

162 the focal herbivore (i.e., the competing species can be either a native or exotic species), we
163 repeated our analysis of the full data set when it was divided into four categories: native focal
164 species and native competitors only, native focal species and exotic competitors only, exotic
165 focal species and native competitors only, and exotic focal species and exotic competitors only.
166 Asking the same questions using these three data sets allows us to fully explore the exotic/native
167 question across multiple ecological contexts while guarding against the “pseudo-rigor” (sensu
168 Englund et al. 1999) of conducting an analysis only on the conservative or four-category data set.
169 Because of the qualitative agreement of these analyses, we focus our discussion on results
170 derived from the full dataset but highlight areas where comparisons of the three different data
171 sets may be informative.

172 **RESULTS**

173 **Summary of the database:** We calculated 1020 effect sizes from 161 papers that
174 reported impact of plant-mediated competition between phytophagous insects (see Supplement).
175 This dataset included 123 different host plant species and a total of 237 insect species from seven
176 orders: Orthoptera (19 species), Hemiptera (95 species), Coleoptera (53 species), Thysanoptera
177 (1 species), Lepidoptera (44 species), Diptera (25 species), and Hymenoptera (11 species). Of
178 these observations, 348 occurred in a laboratory setting, 212 were in a greenhouse, and 458 were
179 in the field. Fail-safe analyses of each response variable in the full dataset showed no evidence of
180 publication bias (all r_s with $P > 0.05$). This was also true for almost all of our analyses of the
181 truncated dataset; only one analysis, the effect of spatial separation on competition with growth
182 as the response variable, showed evidence of publication bias (i.e., r_s with $P < 0.05$; see
183 Appendix).

184 **Do native and exotic herbivores experience different degrees of interspecific**
185 **competition?** While native and exotic herbivores responded differently to interspecific
186 competition, the ‘most successful’ focal insect varied with the response variable examined (Fig.
187 1A). Competition reduced the growth of native herbivores more than the growth of exotic
188 herbivores ($Q_B=14.70$, $P=0.015$). In contrast, competition reduced the fecundity of exotic
189 herbivores more than the fecundity of native species ($Q_B=73.18$, $P=0.001$). There was no impact
190 of native/exotic status on the strength of competition for either survival or development time.
191 These analyses were run looking at native/exotic status regardless of competing herbivore. When
192 we specified the status of both the focal and competing herbivore (i.e. native vs. native, exotic
193 vs. exotic, native vs. exotic, and exotic vs. native) we found almost the same trends as when no
194 competitor was specified (see Table 1S-4S in Supplement 2). When we specify the status of both
195 the focal and competing herbivore and compare the effects of exotic and native competitors, we
196 see that exotic focal herbivores respond similarly to native and exotic competitors in growth,
197 survival, and development time, but they have higher growth rates when competing against a
198 native (Fig. 2B). For native focal herbivores, exotic competitors reduced survival (Fig. 2A;
199 $Q_B=43.80$, $P=0.001$) but positively affected development time ($Q_B=89.58$, $P=0.001$).

200 **Does plant-herbivore coevolutionary history affect interspecific competition?**

201 Competition had a greater negative impact on the growth (Fig. 1B; $Q_B=6.65$, $P=0.028$) and
202 fecundity ($Q_B=22.11$, $P=0.001$) of herbivores that shared a coevolutionary history with their host
203 plant. Coevolutionary history did not alter the impact of competition when assessing herbivore
204 survival or development time.

205 **Does spatial separation affect the strength of competition differently in native and**

206 **exotic insects?** Fecundity and survival of native herbivores were more impacted by competition

207 than exotic herbivores when they spatially co-occurred with the competing herbivore (Fig. 3A;
208 $Q_B=32.77$, $P=0.003$; $Q_B=13.37$, $P=0.005$ respectively). If the focal insect was exotic, spatial co-
209 occurrence did not alter the impact of competition on survival and fecundity. The growth of
210 exotic insects, however, was more impacted by competition when herbivores were spatially
211 separated (Fig. 3B; $Q_B=40.86$, $P=0.002$).

212 **Does temporal separation affect the strength of competition differently in native and**
213 **exotic insects?** Temporal separation had different impacts on native and exotic insects. Native
214 focal insects were negatively impacted by competitive interactions regarding growth and
215 development time (Fig. 4A; $Q_B = 12.75$, 10.93 $P = 0.009$, 0.073). However, exotic insects
216 experiencing interspecific competition were not impacted by temporal separation (Fig. 4B).

217 **DISCUSSION**

218 The results of this meta-analysis demonstrate competitive differences between native and
219 exotic herbivores. For instance, factors such as temporal and spatial separation have a greater
220 impact on how native versus exotic herbivores respond to competition. We also found significant
221 competitive advantages for insects that have not coevolved with their host plant, suggesting that
222 plant-insect coevolutionary history may be a stronger predictor of competitive success.
223 Competitive differences between insects may influence exotic insect establishment and control.

224 **Comparison of native and exotic insects:** We expected exotic herbivores to be
225 competitively superior to native species. Previous work supports this hypothesis, since
226 competitive superiority has been cited as a factor in the success of many exotic species (Sakai et
227 al. 2001). Exotic insects, however, were not consistently better competitors for all measured
228 responses. For example, although competition affected the growth rates of exotic insects more
229 than native insects, the fecundity of exotic insects was less affected (Fig. 2A). While there were

230 no general patterns of competitive superiority, native and exotic insects did respond differently to
231 competition. For instance, native herbivores responded differently to native and exotic
232 competitors, but exotic herbivores were unaffected by the native/exotic status of the competitor
233 (Fig. 2B).

234 There are several reasons why we may not have seen consistent trends in competitive
235 success. One possibility is that the native/exotic status of an insect may not be an important
236 predictor of competition. A similar conclusion was reached in a study of plant competition,
237 which found that native and exotic plant species had no intrinsic differences in competitive
238 abilities (Dawson et al. 2012). Alternatively, our method of classifying exotics may have
239 generated inconsistent responses. This study combined all exotic insects, including those that are
240 invasive, defined as environmentally or economically harmful, and non-invasive, into a single
241 category in order to reach adequate levels of replication. A recent study comparing plant species
242 showed that invasive exotics are competitively superior to non-invasive exotics (Graebner et al.
243 2012). Because the body of literature examining exotic species is likely biased toward invasive
244 rather than non-invasive exotics, our inclusion of all types of exotics in this study may
245 overestimate the impact of exotic species (and, conversely, underestimate the impact of invasive
246 exotic species).

247 **Plant-insect co-evolution:** Many studies explore competition between native/exotic
248 status of herbivores without addressing the herbivores' coevolutionary history with the host
249 plant. Insects that coevolve with their host plants may be more susceptible to plant-induced
250 defenses and plant-mediated competition, while insects lacking a coevolutionary history with
251 their host plant may be better able to overcome or tolerate these effects. If the plant and focal
252 insect originate from the same geographic region, the insect may thus no longer have a

253 competitive advantage regardless of the pairs' current geographic status. Although co-evolved
254 exotic plants and insects may have adapted to the novel environment and may no longer share
255 co-evolved traits, co-evolution is still more likely than between species with no evolutionary
256 history.

257 Our results suggest that plant-insect coevolution is a stronger predictor of competitive
258 success than native/exotic status alone. Insects that co-occur with the host plant in their native
259 range are more negatively affected by interspecific competition than those that do not share a
260 coevolutionary history. When the plant and insect naturally co-occurred in their native range,
261 competition had a greater impact on insect growth and fecundity (Fig. 1B). Thus, plant-
262 insect co-evolution may control native herbivores while allowing for success of non-coevolved
263 exotics (Parker et al. 2006, Gandhi and Herms 2010, Raupp et al. 2010, Desurmont et al. 2011).
264 For example, *Viburnum spp.* that share a coevolutionary history with the leaf beetle *Pyrrhalta*
265 *viburni* have higher production of wound tissue that crush *P. viburni* eggs when compared with
266 *Viburnum spp.* that do not share a coevolutionary history (Desurmont et al. 2011). Additionally,
267 Woodard et al. (2012) found that a moth that had coevolved with *Opuntia* cactus induced
268 significantly more defenses than a moth that had not coevolved with the plant. Although we
269 group native insects on exotic plants and exotic insects on native plants as 'not sharing a co-
270 evolutionary history' it is possible that these two combinations yield different results. By
271 restricting ourselves to comparisons with substantive replication, however, we are not able to
272 separately assess native insect/exotic plant and exotic insect/native combinations. Lack of
273 replication was also responsible for our inability to examine temporal and spatial controls on
274 competition in the context of plant-insect co-evolution.

275 **Spatial separation:** Our data show that native and exotic species respond differently to
276 spatial separation. Spatial separation reduced the effects of competition on native insects. Native
277 herbivores had higher fecundity and survival rates when they fed in a different location than their
278 competitor (Fig. 3A). Niche differentiation by feeding in a different location or on a different
279 plant part may reduce competition. For example, although two species of bark beetle colonize
280 Norway spruce, the inferior competitor is able to persist by aggregating in a different spatial
281 location than the superior competitor (Schlyter and Anderbrant 1993). Additionally, three aphid
282 species, *Euceraphis betulae*, *Callipterinella calliptera*, and *Betulaphis brevopilosa*, coexist on the
283 same plant by feeding on leaves in different phenological states (Hajek and Dahlsten 1986).
284 Although exotic herbivores may respond to spatial separation differently than natives, the trends
285 for exotics were less clear and may be species-specific and dependent on the extent of spatial
286 separation.

287 **Temporal separation:** These results suggest that exotic insects are not significantly
288 impacted by temporal separation. Exotic herbivores had similar competitive outcomes with and
289 without temporal separation (Fig. 4B). If exotic herbivores are able to overcome plant defenses,
290 they may perform equally well even if their competitor is feeding at the same time.

291 In contrast, native herbivores were more affected by competition when they fed on a
292 plant on which a competitor was already present (Fig. 4A). We found that native herbivores had
293 increased development times and reduced growth rates when the insect began feeding after a
294 competitor. Both of these variables are associated with negative impacts on fitness. The slow
295 growth/high mortality hypothesis posits that longer development times on poor hosts may be
296 correlated with higher predation and parasitism rates (Haggstrom and Larsson 1995). Woodard et
297 al. (2012) showed that insects had longer development times on plants with higher levels of

298 defenses. Lower growth in natives arriving after a competing insect may be due to plant-
299 mediated priority effects if the plant responds to the initial insect attack and mounts plant
300 defenses. In support of this, belowground herbivores are only negatively affected by
301 aboveground herbivore feeding when the aboveground herbivore is placed on the plant before
302 the belowground herbivore (Johnson et al. 2012). Continued prior feeding might be necessary to
303 induce systemic defenses.

304 We expect that a long period of temporal separation between focal and competing
305 herbivores will reduce the impact of competition in native insects. We were not able to evaluate
306 different lengths of temporal separation due to low replication. These responses may be unique
307 to each plant-insect association and may depend on the extent of temporal separation.

308 **Conclusions and future research:** Plant-insect coevolutionary history may be as or
309 more useful than native/exotic status when predicting the outcome of interspecific herbivore
310 competition. Due to the importance of plant-mediated effects, native and exotic insects respond
311 differently to interspecific competition. Future research should focus on direct comparisons of
312 insects with and without a coevolutionary history with the host plant. These insights may help
313 guide future invasion control efforts, as herbivore-host coevolutionary history may be an
314 important predictive factor for the impacts of exotic species. As globalization increases species
315 invasions, an understanding of host-herbivore coevolutionary history will become particularly
316 important.

317 **ACKNOWLEDGEMENTS**

318 J. Rafter and R. Casagrande assisted in data collection. The paper benefitted greatly from
319 the comments of two anonymous reviewers and J. Cronin. Finally, we are also grateful to Robert
320 Denno, without whom this work would not have been possible.

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402 **SUPPLEMENTAL MATERIAL**

403 **Supplement 1:** List of all competing insect pairs evaluated and the number of times they were
404 used in the database.

405 Supplement 2: Additional analyses on the importance of coevolutionary history, temporal
406 separation, and spatial separation on interspecific competition when controlling exotic/native
407 status of the focal and competing herbivore.

408 **Appendix A:** Additional description of methods and statistical analysis.

409

410 **FIGURE LEGENDS**

411 Figure 1: The effect of native/exotic status (A) and coevolutionary history (B) on
412 interspecific competition. This dataset assesses competition on growth, fecundity, survival and
413 development time. Mean effect sizes are presented with 95% bootstrap confidence intervals and
414 numbers above error bars are the number of observations per group. The horizontal dotted line at
415 $RR = 1.0$ represents no interspecific competition, < 1 represents competition, and > 1 represents
416 facilitation. Asterisks denote significant differences ($P < 0.05$) between groups.

417 Figure 2. The effect of competitor native/exotic status on interspecific competition when
418 focal species is native (A) and exotic (B). Response variables (growth, fecundity, survival, and
419 development time) are measured on the focal insect when in competition with native/exotic
420 competitors. Mean effect sizes are presented with 95% bootstrap confidence intervals and
421 numbers above error bars are the number of observations per group. I.D. stands for insufficient
422 data.

423 Figure 3: The effect of spatial separation on interspecific competition when herbivore is
424 native (A), and when herbivore is exotic (B). Herbivores are considered spatially separated when
425 competing herbivores are physically separate and do not feed in the same location. Mean effect
426 sizes are presented with 95% bootstrap confidence intervals and numbers above error bars are the
427 number of observations per group. The horizontal dotted line at $RR = 1.0$ represents no
428 interspecific competition, where spatially separated and non-spatially separated herbivores have
429 similar means. Asterisks denote significant differences ($P < 0.05$) between groups. I.D. stands for
430 insufficient data.

431 Figure 4: The effect of temporal separation on interspecific competition when herbivore
432 is native (A), and when herbivore is exotic (B). Herbivores are considered temporally separated

433 when focal herbivore arrives to the host secondarily to the competing herbivore. Mean effect
434 sizes are presented with 95% bootstrap confidence intervals and numbers above error bars are the
435 number of observations per group. The horizontal dotted line at $RR = 1.0$ represents no
436 interspecific competition, where temporally separated and non-temporally separated herbivores
437 have similar means. Asterisks denote significant differences ($P < 0.05$) between groups.

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439 |

440 Figure 1.

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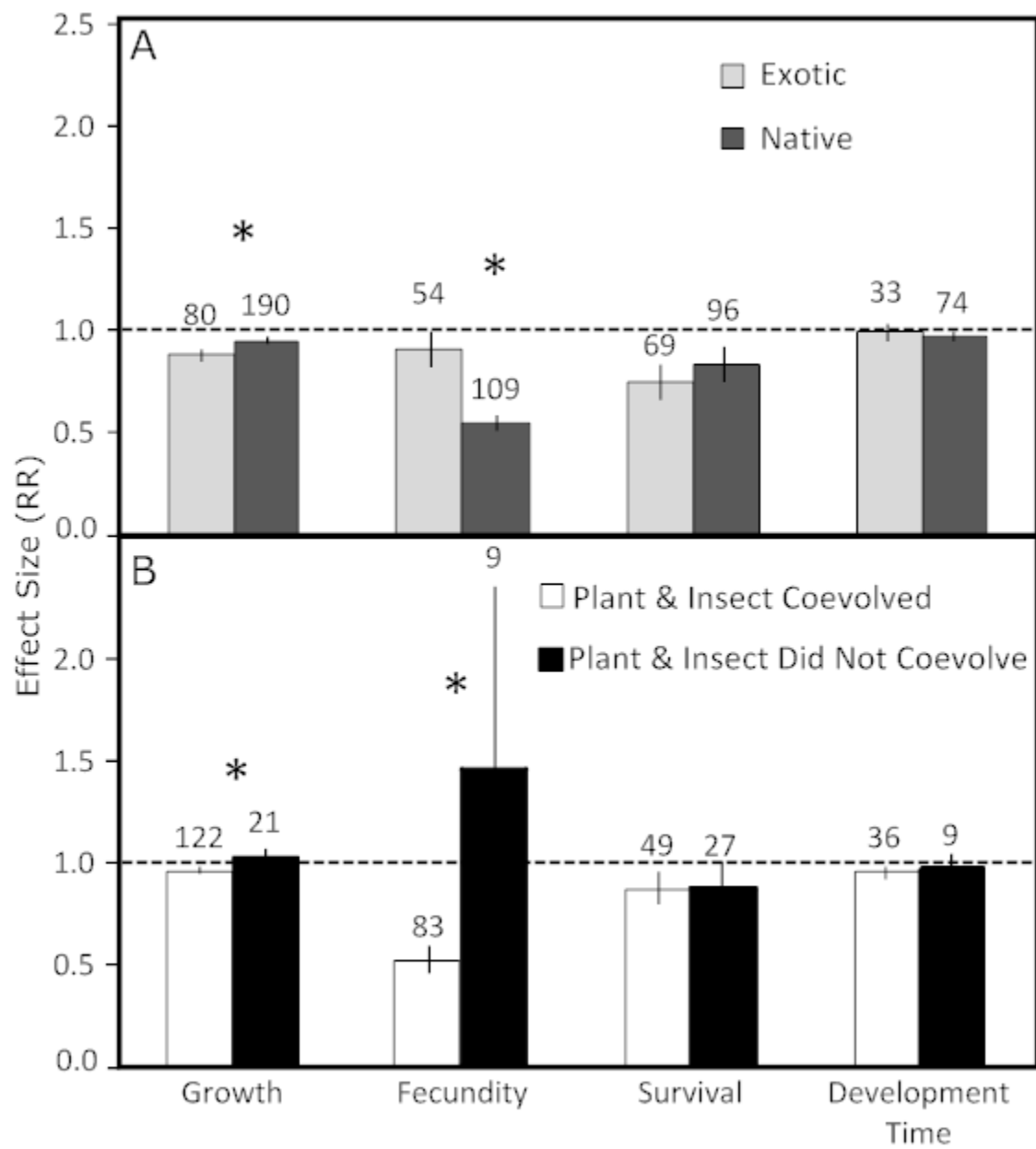


Figure 2.

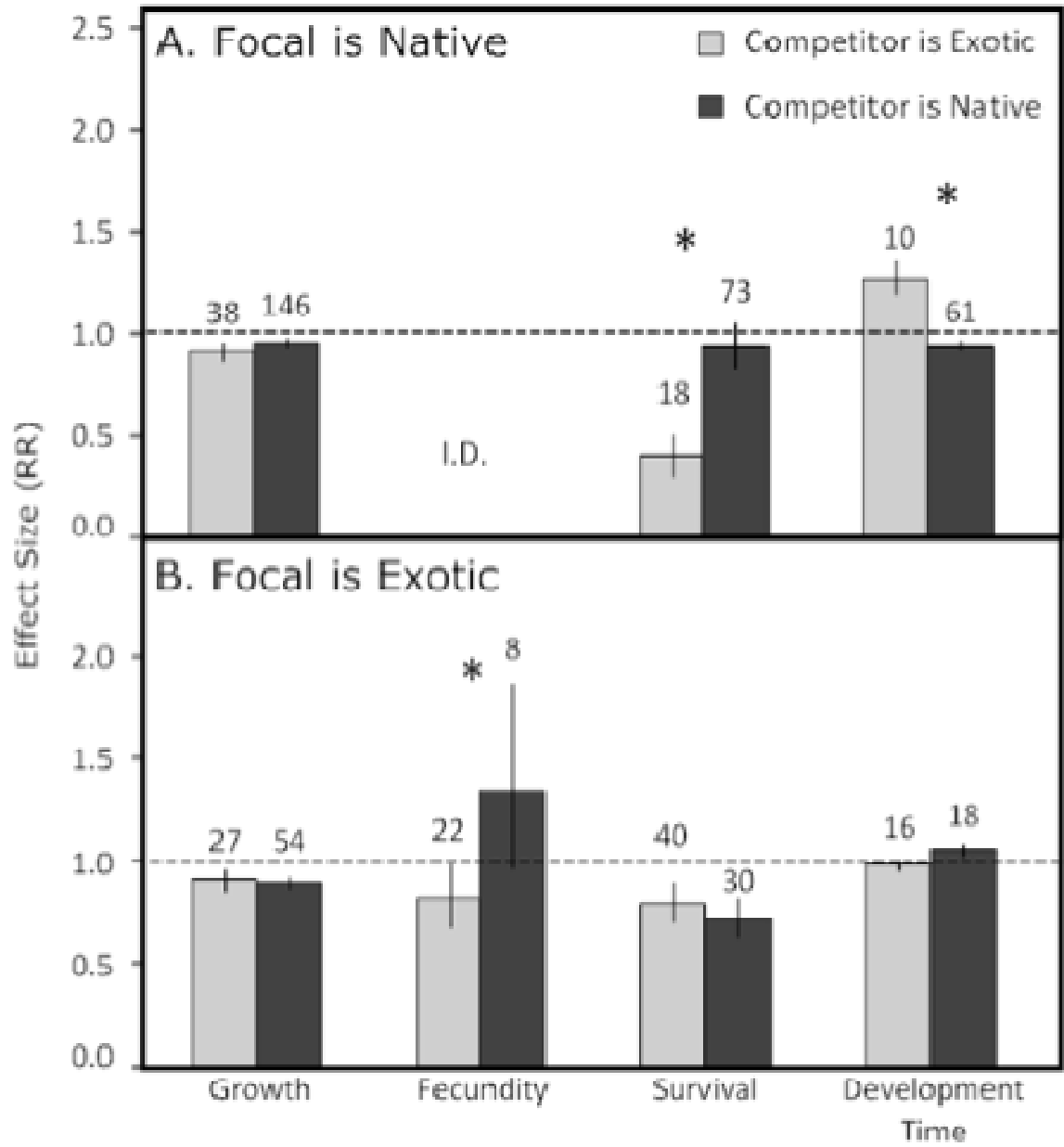
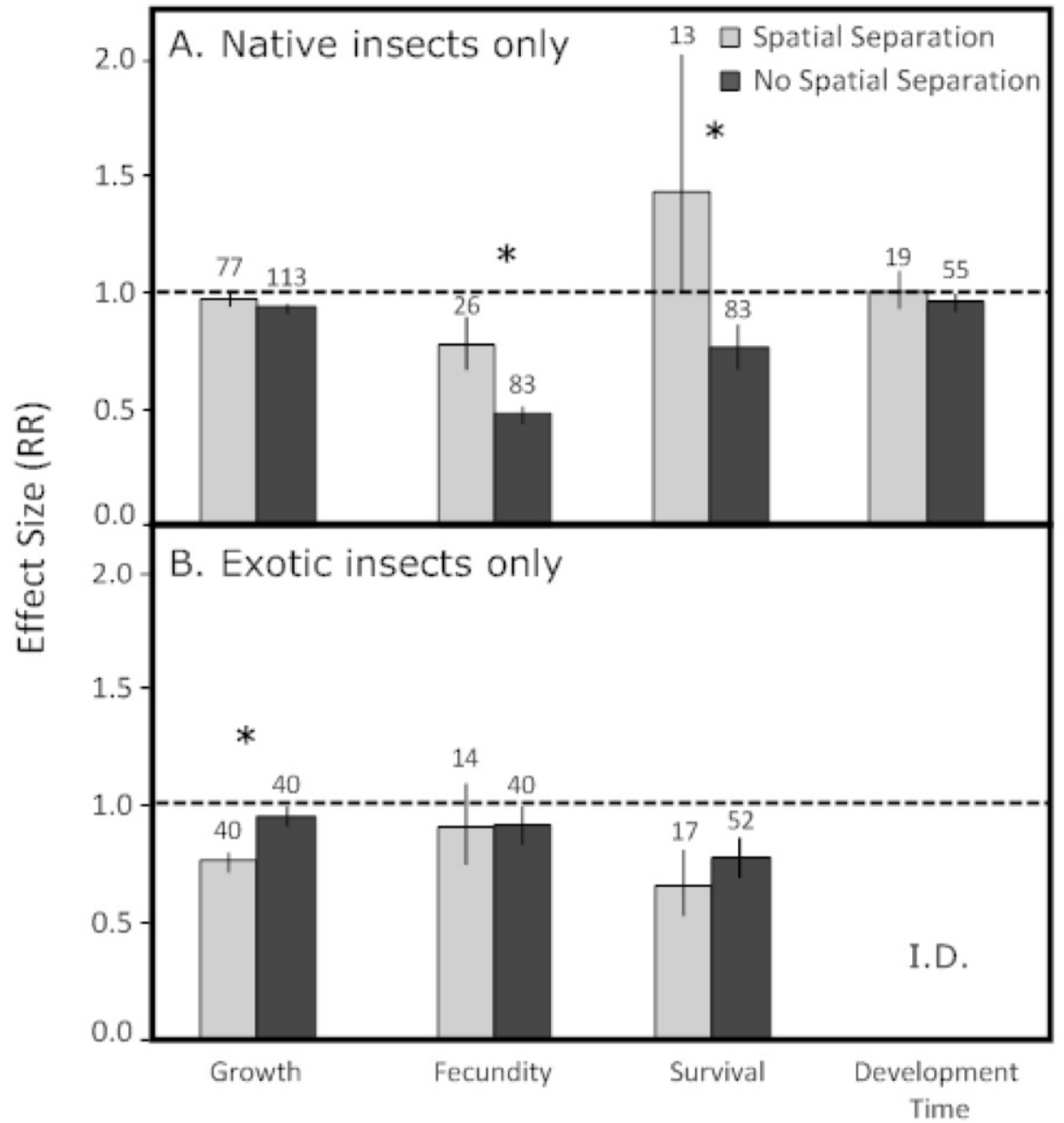


Figure 3.



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