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# Are Exotic Herbivores Better Competitors? A Meta-Analysis

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1      RUNNING HEAD: Competition in exotic herbivores

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12      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

7

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 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 brevipilosa*, 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.

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401

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

**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.
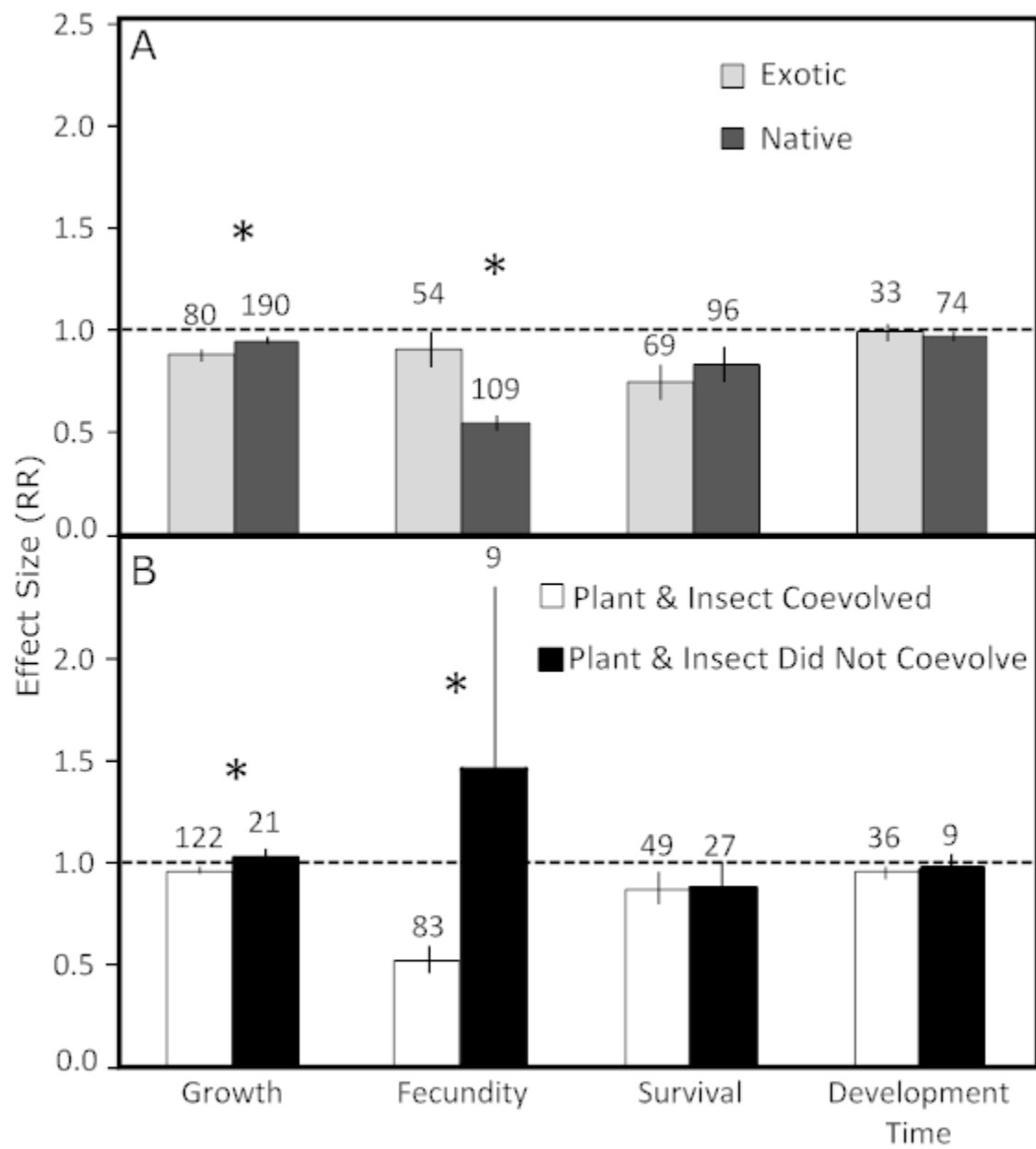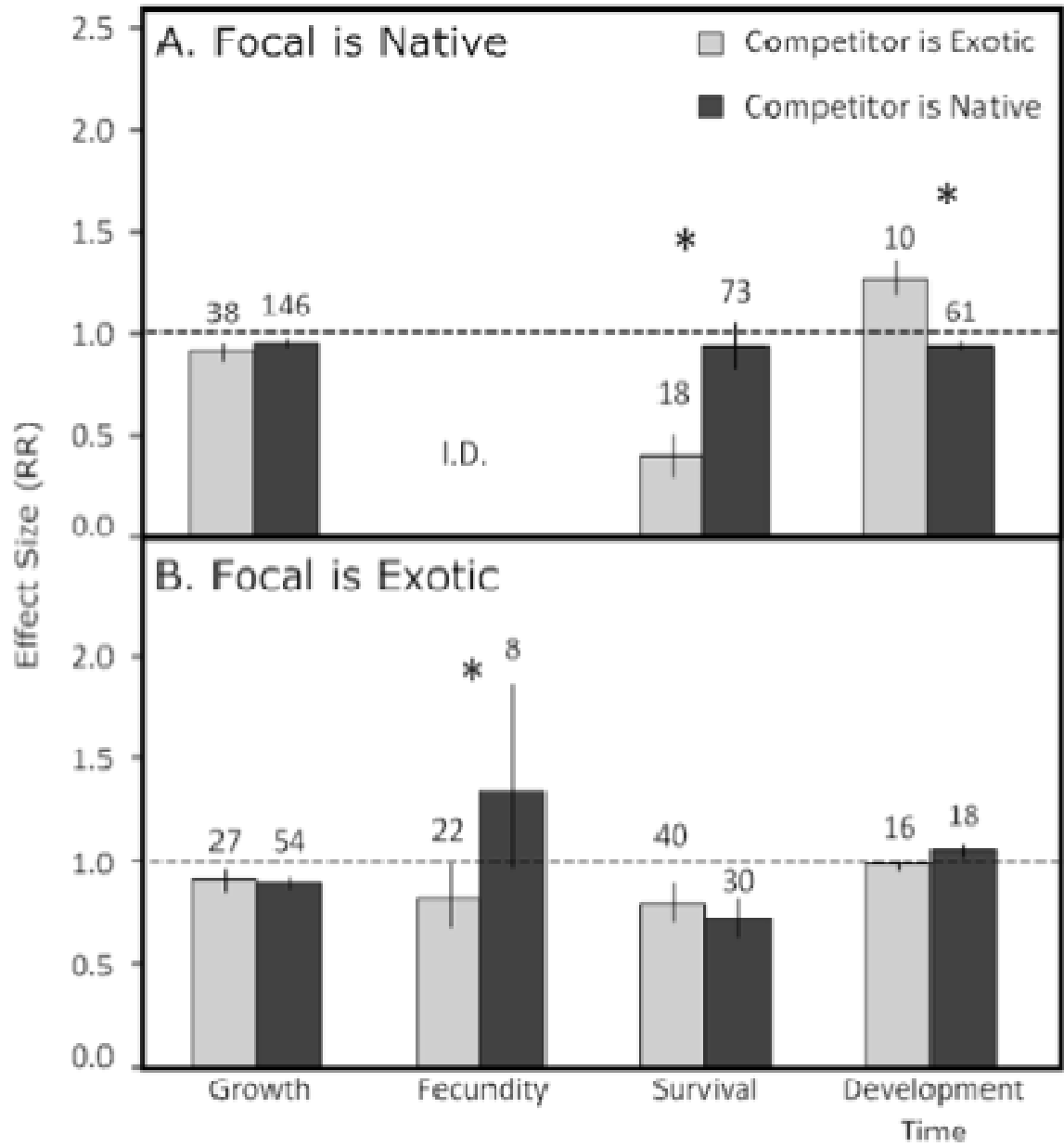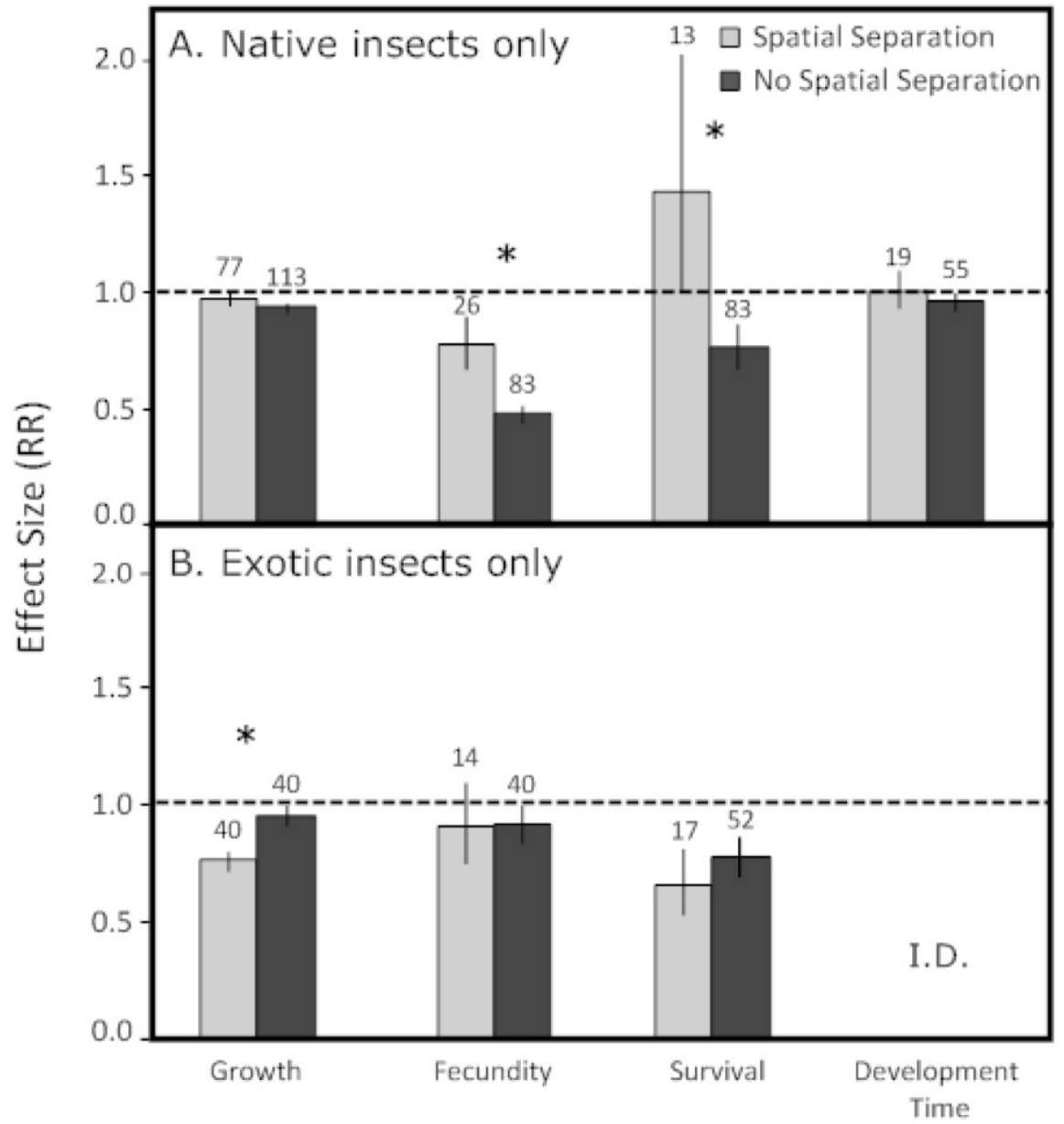
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440    Figure 1.

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