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RUNNING HEAD: Competition in exotic herbivores

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ARE EXOTIC HERBIVORES BETTER COMPETITORS? A META-ANALYSIS

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ABSTRACT:

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

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

INTRODUCTION

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

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

While there are a number of reasons to suspect that exotic species are generally strong interspecific competitors, many examples suggest otherwise. Specifically, the failure of many exotic species to establish and reach high densities may be linked to the competitive dominance of native species. For example, Paini et al. (2008) suggested that the exotic thrips *Frankliniella tritici* cannot reach high densities on the east coast of the United States because it is competitively inferior to the native thrips *F. occidentalis*. More generally, exotic species may be at a competitive disadvantage whenever they are maladapted to the novel ecosystem (Ward-Fear et al. 2009). Despite the large number of studies addressing interspecific herbivore competition for a given pair of species, we lack an overarching sense of whether a species' native/exotic status and coevolutionary history with its host plant affects the outcome of interspecific herbivore competition. We distinguish between these two factors since they are not necessarily correlated; an exotic insect can, for instance, feed on its native host plant outside of both species' native range (something that can occur when the host plant is itself exotic).

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

We present the results of a meta-analysis assessing whether native/exotic status, consumer-host coevolutionary history, and spatiotemporal co-occurrence affect the strength of exploitative competition between herbivorous insects. Such competitive interactions can be thought of as plant-mediated, since they occur when one phytophagous insect indirectly affects another species through the first species' impact on the nutritional and/or chemical content of the plant. We build on an exhaustive database of interactions between insect herbivores compiled by Kaplan and Denno (2007); our restriction to plant-mediated interactions excludes apparent competition and other enemy-mediated interactions from our analysis. The importance of competition to phytophages has been established (Denno et al. 1995); rather than revisit this question, we take a quantitative approach to address the importance of species invasions and evolutionary history to the strength of competition. Our analysis also included two other factors, spatial and temporal separation, known to affect the strength of competition. We examined these issues by addressing the following four questions: (1) Do native and exotic herbivores respond differently to interspecific competition; (2) Does the outcome of competition differ if the host plant and herbivore share a coevolutionary history (i.e., whether or not they co-occur in their native range); (3) Does native/exotic status alter the impact of spatial separation on interspecific herbivore competition; and (4) Does native/exotic status alter the impact of temporal separation on interspecific herbivore competition.

METHODS

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

In order to parallel the methods used in Denno et al. (1995) and Kaplan and Denno (2007), we limited our database to studies evaluating interspecific competition between phytophagous insects. In order to be included in the database, studies had to report the results of plant-mediated interactions in terrestrial systems and assess one or more of the following herbivore variables: growth, development time, fecundity, or survival. We chose these response variables because they are commonly reported in the literature and have been used in previous meta-analyses of plant-herbivore systems (Koricheva et al. 1998, Kaplan and Denno 2007). Each paper had to report mean values for both control (defined as the focal insect's response in the absence of a potential competitor) and experimental (defined as the focal insect's response in the presence of a potential competitor) treatments, some measurement of variation around the mean, and data on within-treatment sample size. Publications from the Kaplan and Denno (2007) meta-analysis that did not meet these criteria were excluded from our analysis.

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

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

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

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

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

We analyzed comparisons 1-4 using both our full data set and a conservative ('truncated') data set that uses one randomly-selected observation for each pair of competing species per response variable. Because these two data sets only specify the native/exotic status of the focal herbivore (i.e., the competing species can be either a native or exotic species), we repeated our analysis of the full data set when it was divided into four categories: native focal species and native competitors only, native focal species and exotic competitors only, exotic focal species and native competitors only, and exotic focal species and exotic competitors only. Asking the same questions using these three data sets allows us to fully explore the exotic/native question across multiple ecological contexts while guarding against the "pseudo-rigor" (sensu Englund et al. 1999) of conducting an analysis only on the conservative or four-category data set. Because of the qualitative agreement of these analyses, we focus our discussion on results derived from the full dataset but highlight areas where comparisons of the three different data sets may be informative.

RESULTS

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

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

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

Does spatial separation affect the strength of competition differently in native and exotic insects? Fecundity and survival of native herbivores were more impacted by competition than exotic herbivores when they spatially co-occurred with the competing herbivore (Fig. 3A; Q_B=32.77, P=0.003; Q_B=13.37, P=0.005 respectively). If the focal insect was exotic, spatial co-occurrence did not alter the impact of competition on survival and fecundity. The growth of exotic insects, however, was more impacted by competition when herbivores were spatially separated (Fig. 3B; Q_B=40.86, P=0.002).

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

DISCUSSION

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

Comparison of native and exotic insects: We expected exotic herbivores to be competitively superior to native species. Previous work supports this hypothesis, since competitive superiority has been cited as a factor in the success of many exotic species (Sakai et al. 2001). Exotic insects, however, were not consistently better competitors for all measured responses. For example, although competition affected the growth rates of exotic insects more than native insects, the fecundity of exotic insects was less affected (Fig. 2A). While there were no general patterns of competitive superiority, native and exotic insects did respond differently to competition. For instance, native herbivores responded differently to native and exotic competitors, but exotic herbivores were unaffected by the native/exotic status of the competitor (Fig. 2B).

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

Plant-insect co-evolution: Many studies explore competition between native/exotic status of herbivores without addressing the herbivores' coevolutionary history with the host plant. Insects that coevolve with their host plants may be more susceptible to plant-induced defenses and plant-mediated competition, while insects lacking a coevolutionary history with their host plant may be better able to overcome or tolerate these effects. If the plant and focal insect originate from the same geographic region, the insect may thus no longer have a competitive advantage regardless of the pairs' current geographic status. Although co-evolved exotic plants and insects may have adapted to the novel environment and may no longer share co-evolved traits, co-evolution is still more likely than between species with no evolutionary history.

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

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

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

In contrast, native herbivores were more affected by competition when they fed on a plant on which a competitor was already present (Fig. 4A). We found that native herbivores had increased development times and reduced growth rates when the insect began feeding after a competitor. Both of these variables are associated with negative impacts on fitness. The slow growth/high mortality hypothesis posits that longer development times on poor hosts may be correlated with higher predation and parasitism rates (Haggstrom and Larsson 1995). Woodard et al. (2012) showed that insects had longer development times on plants with higher levels of defenses. Lower growth in natives arriving after a competing insect may be due to plant-mediated priority effects if the plant responds to the initial insect attack and mounts plant defenses. In support of this, belowground herbivores are only negatively affected by aboveground herbivore feeding when the aboveground herbivore is placed on the plant before the belowground herbivore (Johnson et al. 2012). Continued prior feeding might be necessary to induce systemic defenses.

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

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

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Supplemental Material

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

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

Appendix A: Additional description of methods and statistical analysis.

Figure Legends

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

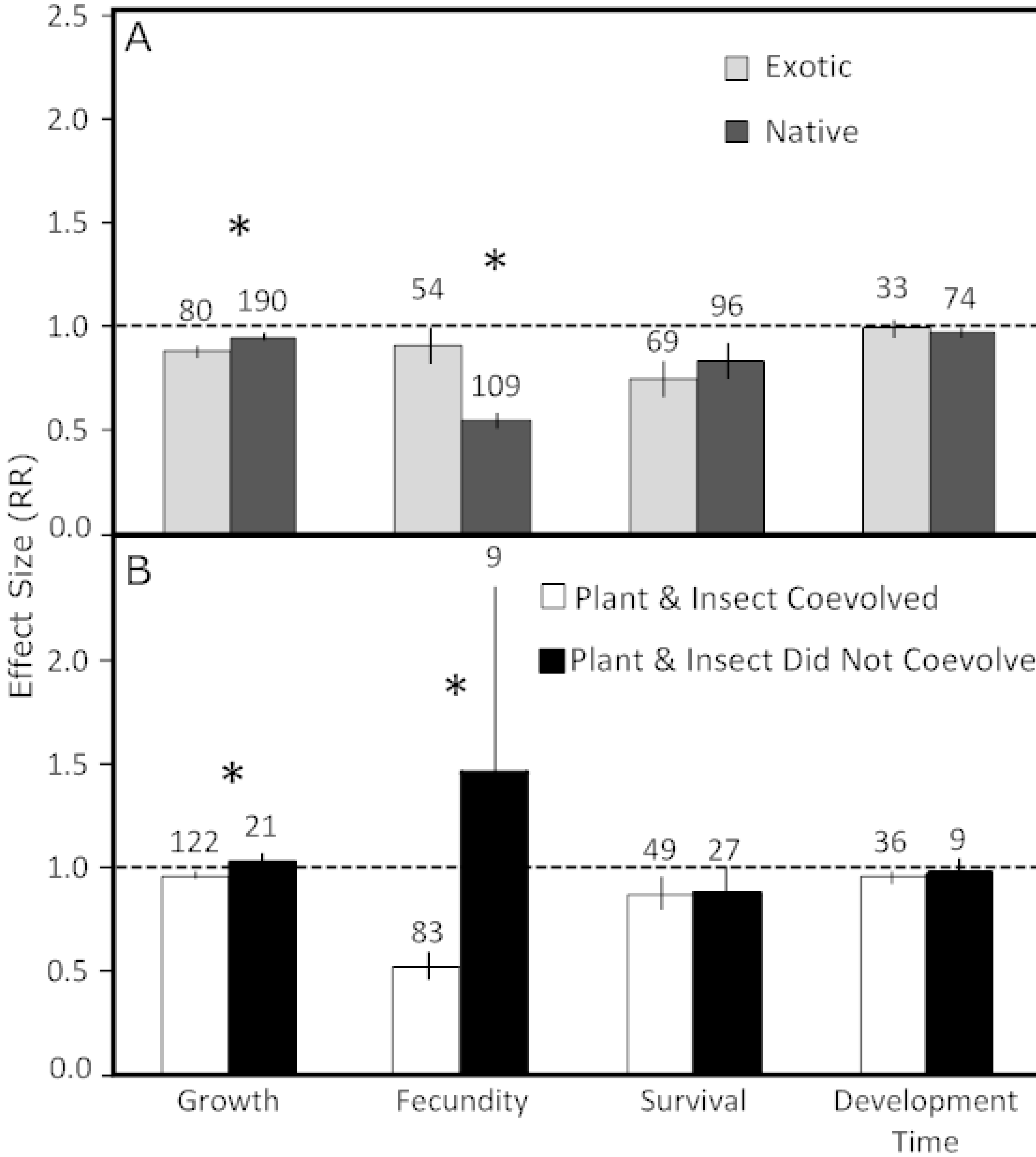
Figure 2. The effect of competitor native/exotic status on interspecific competition when focal species is native (A) and exotic (B). Response variables (growth, fecundity, survival, and development time) are measured on the focal insect when in competition with native/exotic competitors. Mean effect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

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

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

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

Figure 1.



A
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Plant & Insect Did Not Coevolve
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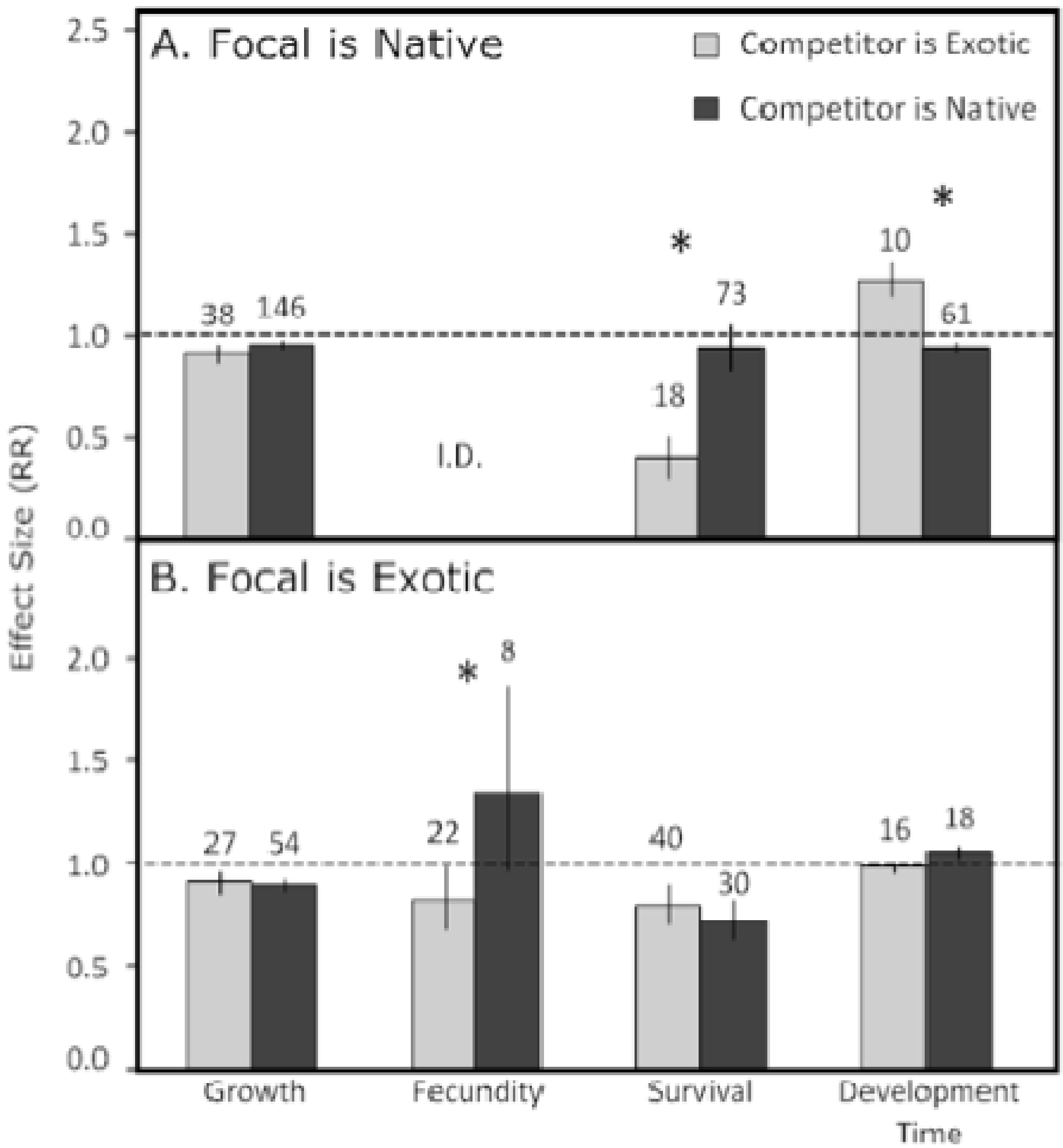
Effect Size (RR)
2.5
2.0
1.5
1.0
0.5
0.0
Growth
Fecundity
Survival
Development Time

Figure 2.



A. Focal is Native
Competitor is Exotic
Competitor is Native
B. Focal is Exotic
Effect Size (RR)
2.5
2.0
1.5
1.0
0.5
0.0
38
146
I.D.
18
73
10
61
*
*
27
54
22
8
*
40
30
16
18
Growth
Fecundity
Survival
Development
Time

Figure 3.

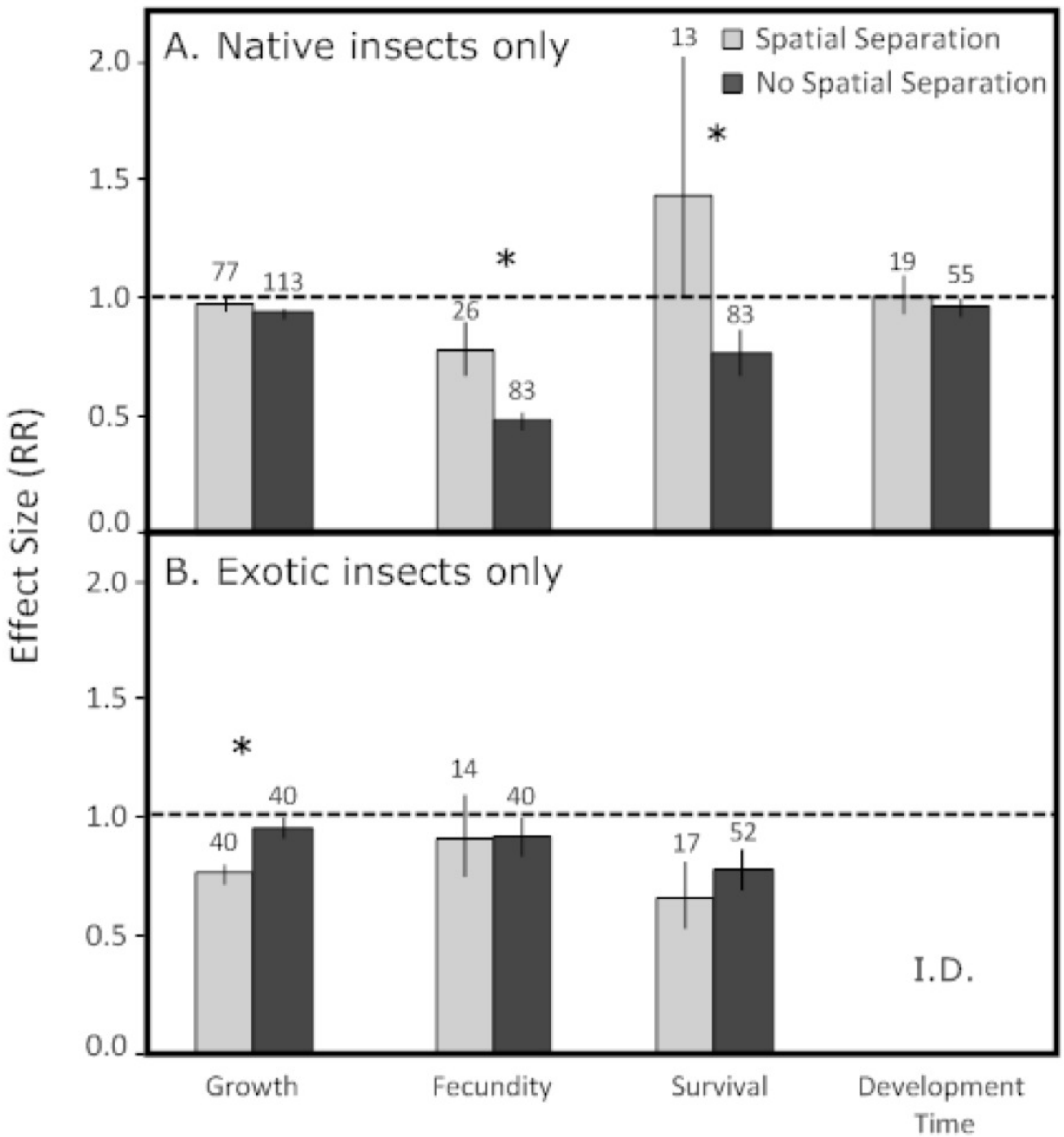
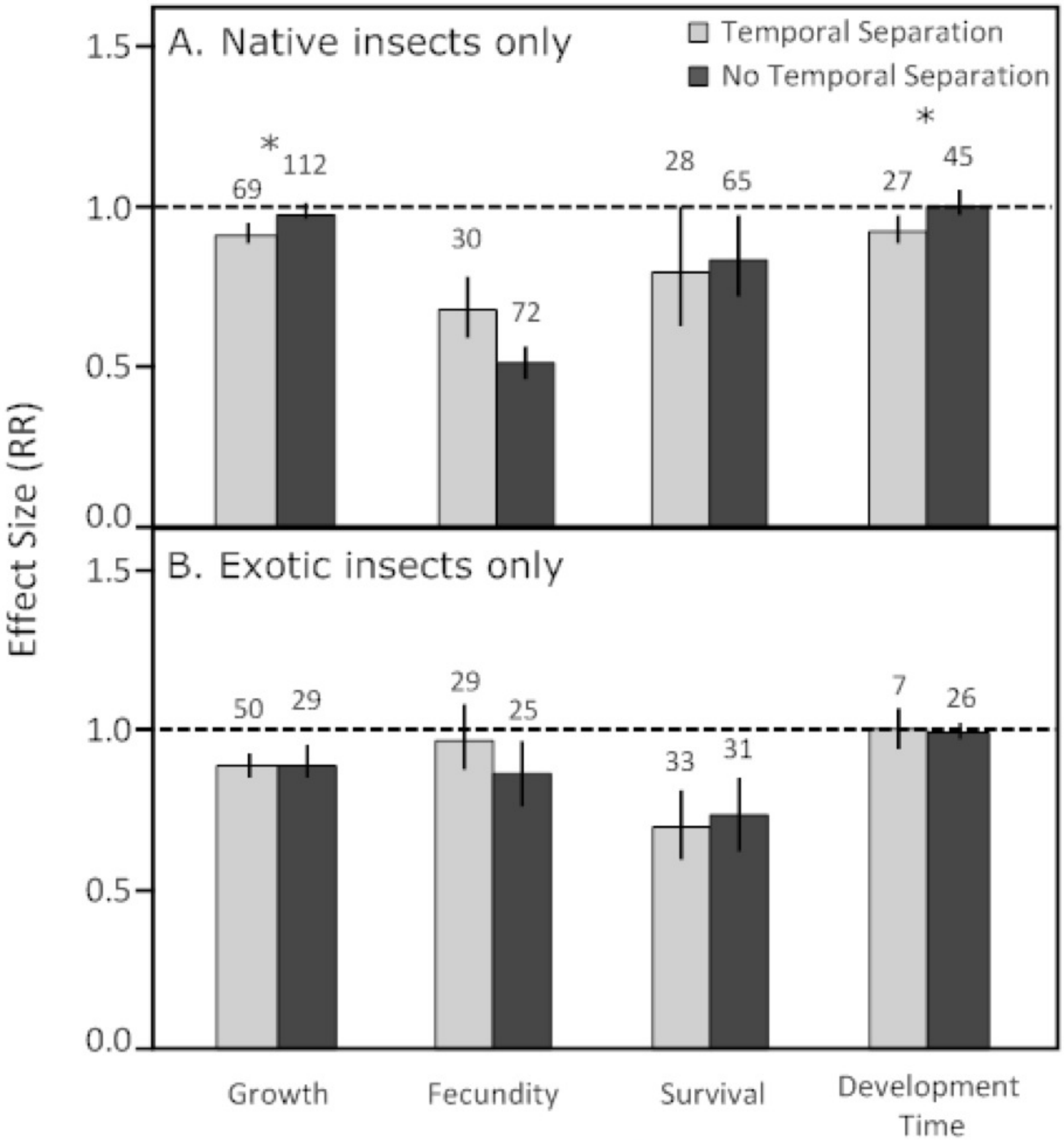

A. Native insects only
B. Exotic insects only
Spatial Separation
No Spatial Separation
Effect Size (RR)
2.0
1.5
1.0
0.5
0.0
77
113
26
83
13
83
19
55
40
40
14
40
17
52
*
I.D.
Growth
Fecundity
Survival
Development Time

Figure 4.


A. Native insects only
Temporal Separation
No Temporal Separation
B. Exotic insects only
Effect Size (RR)
1.5
1.0
0.5
0.0
69
112
30
72
28
65
27
45
50
29
29
25
33
31
7
26
*
*
Growth
Fecundity
Survival
Development Time