

**REVIEW AND
SYNTHESIS****Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory**

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Abstract

The importance of interspecific competition is a highly controversial and unresolved issue for community ecology in general, and for phytophagous insects in particular. Recent advancements, however, in our understanding of indirect (plant- and enemy-mediated) interactions challenge the historical paradigms of competition. Thus, in the context of this rapidly developing field, we re-evaluate the evidence for interspecific competition in phytophagous insects using a meta-analysis of published studies. Our analysis is specifically designed to test the assumptions underlying traditional competition theory, namely that competitive interactions are symmetrical, necessitate spatial and temporal co-occurrence, and increase in intensity as the density, phylogenetic similarity, and niche overlap of competing species increase. Despite finding frequent evidence for competition, we found very little evidence that plant-feeding insects conform to theoretical predictions for interspecific competition. Interactions were highly asymmetrical, similar in magnitude within vs. between feeding guilds (chewers vs. sap-feeders), and were unaffected by the quantity of resources removed (% defoliation). There was mixed support for the effects of phylogeny, spatial/temporal separation, and the relative strength of intra- vs. interspecific competition. Clearly, a new paradigm that accounts for indirect interactions and facilitation is required to describe how interspecific competition contributes to the organization of phytophagous insect communities, and perhaps to other plant and animal communities as well.

Keywords

Community diversity, competitive exclusion, density dependence, feeding guild, interspecific competition, intraspecific competition, meta-analysis, niche, population regulation, resource partitioning.

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INTRODUCTION

Competition is routinely cited as one of the primary biotic factors that shape patterns of distribution, abundance and diversity in ecological communities (Begon *et al.* 2005). The prominent status of competition in modern ecology is undoubtedly linked with views espoused by early ecologists, many of whom were strong advocates for the central role of competitive interactions between species (Darwin 1859; Grinnell 1917; Volterra 1926; Clements *et al.* 1929; Lotka 1932; Nicholson 1933; Gause 1934). Importantly, most biologists that are now lauded for developing and promoting traditional competition theory studied a diverse range of

taxonomic groups (e.g. Clements – plants; Grinnell, Lack, MacArthur – birds; Gause – *Paramecium*; Connell – marine invertebrates; Schoener, Pianka – reptiles). Entomologists, however, were not well-represented, although several insect ecologists including Nicholson and Andrewartha provided important contributions in the debate over density-dependence. This point is noteworthy because plant-feeding insects have become focal organisms for studies on population dynamics and community diversity. Because competition is deeply ingrained in ecological theory, it became widely accepted as a factor organizing insect assemblages, despite the fact that empirical evidence supporting competition was mostly derived from plant,

vertebrate, and marine systems (Connell 1983; Schoener 1983; Jermy 1985; Denno *et al.* 1995). These circumstances set the stage for what has become a long and controversial debate over the importance of interspecific competition in structuring communities of phytophagous insects.

Initial support for the strength of competitive interactions came from observations of resource partitioning and niche segregation (see references in Denno *et al.* 1995). Investigations of two or more co-occurring and closely related insects revealed subtle yet distinct differences in phenology (i.e. temporal displacement) and feeding location (i.e. within-plant distribution), differences that were largely viewed as divergent strategies permitting stable coexistence (Schoener 1974; Connell 1980). Additionally, one of the best early examples of competitive exclusion came from Park's classic studies on *Tribolium* flour beetles (Park 1948). At the farthest extreme, Janzen (1973) considered all insects sharing a common host plant to be in competition with one another, regardless of niche overlap or ecological similarity: 'In short, a butterfly larva that eats shoot tips can be in very intense competition with a root-eating beetle larva, even though neither is common, neither eats much of its respective plant part, neither comes in contact with each other, neither feeds on the same individual plant, and neither feeds at the same time of the year'.

This view was certainly not shared by most ecologists. Davidson & Andrewartha (1948) were among the first to challenge the importance of competition based on their long-term observations of thrips on rose bushes. Interannual variation in the abundance of thrips was correlated with weather, and not explained by density-dependent factors such as competition. Later theoretical work by Hairston *et al.* (1960) argued that natural enemies regulate herbivores at low densities, green plant material (i.e. food) is plentiful, and therefore competition for resources must be rare at the second trophic level. The final line of anti-competition reasoning was based on the following observations: (i) coexistence of multiple herbivores in spite of extensive niche overlap, (ii) lack of aggression among heterospecifics, or displays of 'harmonious coexistence', (iii) positive density associations between competing species, and (iv) plants with under-utilized or vacant niches, leading to unsaturated communities (Ross 1957; Rathcke 1976; Lawton 1982, 1984; Strong 1982). As a result, interspecific competition was heavily criticized and relegated to a weak and infrequent force in phytophagous insects (Lawton & Strong 1981; Connell 1983; Schoener 1983; Lawton & Hassell 1984; Strong 1984; Strong *et al.* 1984; Jermy 1985).

As previously noted (Denno *et al.* 1995; Denno & Kaplan 2007), many of the arguments surrounding competition (both for and against) were not based on experimental field data, but rather insights that were inferred from patterns

observed in nature. Beginning in the 1980s, however, a series of experimental studies emerged that provided robust support for competition involving herbivorous insects (e.g. Faeth 1986; Harrison & Karban 1986; Karban 1986, 1989). Moreover, several of these examples involved temporally or spatially separated species in different feeding guilds, suggesting that traditional resource-based competition theory may severely underestimate the frequency and intensity of within trophic level interactions. This sudden increase in experimental support prompted a reversal in thinking and competition was thus reinstated as a central factor in the community ecology of phytophagous insects (Faeth 1987, 1988; Damman 1993; Denno *et al.* 1995). Most notably, Denno *et al.* (1995) found evidence for competition occurring in 76% of all pair-wise interactions reported in published studies.

The purpose of this review is to quantitatively assess whether herbivorous insects conform to the traditional paradigm of interspecific competition. Although several previous authors have addressed this issue (Damman 1993; Denno *et al.* 1995), we re-evaluated the evidence for two primary reasons. First, earlier quantitative reviews employed a simple vote-counting approach, which does not allow for the rigorous testing of hypotheses offered by modern meta-analytical techniques (Rosenberg *et al.* 2000; Gates 2002). Second, and perhaps most importantly, the literature on interspecific interactions has changed greatly. Namely, indirect effects involving plants (i.e. induced defenses) and natural enemies (i.e. apparent competition) are far more prevalently encountered in published studies over the past 10 years (Chaneton & Bonsall 2000; Ohgushi 2005; van Veen *et al.* 2006; Denno & Kaplan 2007). Indirect effects clearly violate many of the basic assumptions regarding interspecific competition. Indeed, some of the earliest and harshest criticism of competition came before inducible plant defenses were widely recognized: 'Theoretically, induced defences open up the possibility of two species competing even though they occur on the host at different times, and/or exploit different parts of that host. There is no hard evidence that this does happen, but it is an interesting possibility' (Strong *et al.* 1984).

Competition theory predicts that two organisms engage in a reciprocal struggle for resources and these interactions become more intense as density, spatiotemporal co-occurrence, and ecological similarity (e.g. feeding guild, phylogenetic relatedness) increase. Therefore, our study is specifically designed to test each of these conditions using a meta-analysis of the literature on interspecific interactions among plant-feeding insects. Specifically, we calculated effect sizes to quantitatively evaluate the: (i) effect of herbivore damage (i.e. defoliation) on competitive strength, (ii) magnitude of intra- vs. interspecific competition, (iii) impact of phylogenetic similarity on

competitive strength, (iv) magnitude of within vs. between feeding guild interactions, (v) consequences of spatial and temporal resource partitioning for competitive strength, and (vi) symmetry of interactions between competing species. Overall, our results suggest that by considering indirect interactions, forces such as competition and facilitation will play an increasingly important role in structuring phytophagous insect communities, albeit in non-traditional ways.

METHODS

Criteria for identifying and selecting studies

Published studies that test for interspecific competition in phytophagous insects were compiled using several different approaches. First, we surveyed the cited literature from published reviews on insect competition (Damman 1993; Denno *et al.* 1995), as well as reviews that dealt specifically with indirect plant- and enemy-mediated herbivore interactions (Karban & Baldwin 1997; Chaneton & Bonsall 2000; Ohgushi 2005; van Veen *et al.* 2006; Denno & Kaplan 2007). Next, we used the searchable database Web of Science to identify all studies that cited classic competition review papers. For example, Denno *et al.* (1995) provide the most comprehensive analysis available on competition involving herbivorous insects. Therefore, any recent (the past 10 years) study on insect competition will have likely cited this article. Last, we performed keyword searches on Web of Science using various combinations of the following terms: interspecific competition, insect herbivore, induced plant defense, induced plant resistance, plant-mediated interactions, enemy-mediated interactions, apparent competition, interference competition, exploitative competition.

Unfortunately not all published accounts of insect herbivore competition could be used in our analysis. We specifically sought studies that compared the abundance, emigration, preference (feeding, oviposition), performance (survival, development time, relative growth rate, body size, fecundity), or feeding damage of one herbivore species in the presence and absence of a second herbivore species. Moreover, because these studies were being used for meta-analysis we only included experiments that provided means, measures of variation (standard error, standard deviation) and sample sizes for both control and treatment groups. As our interest was exclusively in herbivorous insects we did not include papers on competition involving non-insect arthropods (e.g. mites) or pollen- and nectar-feeders. We also excluded studies that used mechanical damage to simulate herbivory. Given the above criteria, our search resulted in a total of 333 observations of interspecific herbivore interactions obtained from 145 published studies

(see Appendix S1 for a list of all studies used in meta-analysis).

Calculating and compiling effect sizes

The impact of interspecific competition on herbivore abundance, preference, performance, and/or damage was quantified by calculating an effect size (Hedges' *d*) for each pair-wise species interaction (see Appendix S2 for effect size table). The control group was designated as the competition-free environment, whereas the treatment group was exposed to competitors (except for development time which was reversed to standardize results with other performance-related variables, i.e. an increase in development time produces a negative effect size). As a result, negative effect sizes indicate that the competing species adversely affects the focal herbivore, and the larger the effect size, the greater the magnitude of the competitive impact.

In addition to calculating effect sizes for each individual response variable (e.g. abundance, survival), we also pooled response variables to create a single composite effect size that assessed the overall consequence for each pair-wise species interaction. To do this, we performed a meta-analysis on all of the response variables measured and used the resulting effect size and variance as an estimate of the total herbivore response. In other words, if an experiment quantified the impact of herbivore 1 on the development time, pupal weight, and fecundity of herbivore 2, then we conducted a meta-analysis on these three response variables to generate a single effect size for this interaction. By pooling the values to create a single common response variable, we were able to use all of the available data without pseudoreplication.

Each unique pair-wise herbivore interaction was considered an observation in our dataset. For example, if a study examined the impact of early-season caterpillar defoliation (species 1) on two late-season caterpillars (species 2 and 3), these were scored as two separate observations (i.e. effects of 1 on 2, and 1 on 3). Additionally, because plant traits often mediate interspecific competition (Denno & Kaplan 2007), we considered herbivore interactions as separate observations if they were tested on different plant species. For instance, if competition between two species was examined concurrently on oak and willow trees, then we scored the pair-wise interaction on oak independently of the interaction on willow.

There were only two conditions in which we violated the above criteria. First, when different authors reported on the same interaction these cases were considered separate observations rather than pooled because of the substantial methodological differences employed between studies (this circumstance was exceedingly rare in our dataset). If the same author, however, reported on the same interaction

across multiple publications, then the response was pooled and considered a single observation. The second condition for violating the above criteria involved differences in experimental design. If competition was assessed under fundamentally different ecological circumstances then we separated rather than pooled the observations. Typically, this involved aspects of temporal or spatial segregation. For example, several studies compared the competitive impact of two species reared contemporaneously vs. when they were raised in spatial or temporal isolation from one another (i.e. prior infestation and subsequent removal of one of the two species). Because these experiments represent drastically different competitive conditions, they were considered unique observations in our dataset. However, we pooled responses into a single observation in all other circumstances (e.g. field and greenhouse assessments, competition under varying nutrient/water regimes, etc.).

To test if taxonomic affiliation or herbivore feeding guild affected the strength of competitive interactions (=effect size), we classified each herbivore species by taxonomy (order, family, genus, species) and feeding guild (chewer or sap-feeder). Additionally, the extent of plant damage was noted if such information was provided by the study. This value was calculated (and typically reported) as the percentage of leaf area removed from the plant, rather than absolute quantity of tissue damaged. Thus, the impact of plant damage on competitive strength could only be determined for cases where the competitor was a chewing insect. Although we recognize that spatial variation in leaf-tissue quality and feeding compensation in herbivores may clutter the relationship between percent defoliation and competition, the relationship remains a tenet of competition theory and thus we tested it with the only available data. We did not attempt to quantify herbivory for sap-feeding insects because their feeding damage is often unapparent and, unlike defoliation, herbivore density is difficult to standardize across taxonomic groups. Last, we assessed whether the pair-wise interaction involved herbivores that were feeding at the same time and place (direct interactions), compared with cases where the herbivores were spatially and/or temporally separated from one another (indirect interactions).

In addition to calculating effect sizes for interspecific competitors, we also scored intraspecific interactions for the sub-set of studies that assessed both inter- and intraspecific competition. However, we did not evaluate all published accounts of intraspecific competition; it was only assessed when included as part of a study on interspecific competition. This allowed for a direct comparison of the relative strengths of competition occurring within vs. between species.

For studies that used reciprocal designs (i.e. those that measured the impact of species 1 on 2, and also the impact

of species 2 on 1), we quantified the symmetry of this relationship. Reciprocal interactions were paired and the larger of the two effect sizes was used to define the dominant competitor, whereas the smaller effect size defined the inferior competitor. If interactions were symmetrical then these two effect sizes should be equal in magnitude. Oftentimes reciprocal interactions were tested using temporally separated species whereby plants were previously damaged by species 1 and subsequently offered to species 2, and vice versa. Consequently, the relative symmetry of interspecific competition was assessed for the full dataset, as well as independently for both direct and indirect interactions.

Statistical analysis

The meta-analytical program *MetaWin 2.0* was used to calculate effect sizes and conduct the overall analysis (Rosenberg *et al.* 2000). Sample size dictated which response variables were statistically analysed and thus which data are presented. For categorical models, we only analysed response variables that included > 5 observations per group. Similarly, for continuous models (regression) we used response variables with > 10 observations. As a result, our analyses are robust to spurious conclusions that can be generated from small sample size (Gates 2002).

Mixed-effects models were used throughout, as advocated in recent publications (Gurevitch & Hedges 1999; Rosenberg *et al.* 2000). Resampling tests (999 iterations) were performed to generate cumulative effect sizes with 95% bootstrap confidence intervals. This approach is suggested to account for the violation of basic distributional assumptions (e.g. normality) that typically occurs with meta-analytical data (Adams *et al.* 1997; Gurevitch & Hedges 1999). To account for the problem of multiple comparisons that inflate the probability of committing a type-I error, we used the more conservative $P = 0.01$ value as our cut-off for statistical significance (Gates 2002).

Initially, we analysed the entire dataset using a model with no data structure to determine the grand mean effect size and confidence intervals for each individual response variable. This allows for an overall assessment of the strength of interspecific interactions and potential differences in the magnitude of competition across response variables (i.e. Does competition have a stronger impact on fecundity compared with abundance?).

Next, we used continuous and categorical models to test fundamental assumptions underlying competition theory. First, weighted least squares regressions were used to assess the impact of resource removal (% defoliation) by species 1 on the composite effect size for species 2. Separate regressions were run for herbivores feeding on herbs, woody plants, and the pooled total. Categorical models were

used in all subsequent analyses to compare effect sizes between groups of predictor variables. Specifically, we used the following pre-planned contrasts: (i) intra- vs. interspecific competition, (ii) direct interactions (i.e. no separation) vs. interactions between spatially and/or temporally separated species, (iii) closely vs. distantly related species, (iv) within vs. between feeding guilds, and (v) dominant vs. inferior competitors (i.e. symmetry; see figure legends for additional details on between group contrasts). For each group a mean effect size (d_+) was calculated and reported with 95% bootstrap confidence intervals; effects are considered statistically significant if confidence intervals do not bracket zero. Between-group heterogeneity (Q_B) was tested against a chi-square distribution to determine if significant differences exist among groups of predictor variables.

To address the 'file-drawer problem' whereby non-significant effects are less-likely to be published, we used Rosenthal's Method ($\alpha = 0.05$) to calculate fail-safe values for each variable in the dataset (Rosenberg *et al.* 2000). This estimates the number of non-significant observations that are needed to change the outcome from significant to non-significant. Additionally, we created and visually assessed weighted histograms, funnel plots, and normal quantile plots for each variable to identify potential publication bias and abnormalities in the data structure (Rosenberg *et al.* 2000).

We found little evidence for publication bias in the dataset. Fail-safe values tended to be large, indicating that our analyses are robust to the file-drawer effect (fail-safe = 235, 82, 94, 359, 256, 2382, 2184, 361, respectively, for development time, relative growth rate, body size, survival, oviposition, fecundity, abundance, plant damage). Similarly, weighted histograms, funnel plots, and normal quantile plots did not indicate abnormalities in the data structure.

RESULTS

Evidence for interspecific herbivore interactions was detected in 73% (243/333) of all interactions in our dataset. The majority of observations (62%; 205/333 interactions) documented competition, whereas fewer cases provided evidence for facilitation (11%; 38/333). The mean effect size for each response variable was significantly less than zero in the overall analysis (none of the confidence intervals overlap zero), but the magnitude of the effects varied greatly (Fig. 1). An effect size of 0.2 is considered small, 0.5 moderate and 0.8 large (Cohen 1988). Therefore, competition had weak effects on body size (-0.2448) and plant damage (-0.2790), moderate effects on abundance (-0.5398), survival (-0.4502), development time (-0.6432) and relative growth rate (-0.4579), and large effects on fecundity (-1.0393) and oviposition preference (-0.8816).

Defoliation intensity by leaf-chewing insects had no impact on the effect size of heterospecific competitors ($Q_{reg} = 0.43$, $P = 0.5102$, $n = 64$; Fig. 2). The mean effect size was significantly less than zero ($d_{++} = -0.4081$), indicating that leaf damage adversely affected subsequent herbivores. However, the slope of the regression did not differ from zero, suggesting that the quantity of tissue removed did not affect the strength of interspecific competition. Likewise, separate regressions for leaf-chewing herbivores feeding on herbs ($Q_{reg} = 0.37$, $P = 0.544$, $n = 49$) and woody plants ($Q_{reg} = 0.42$, $P = 0.516$, $n = 15$) were also non-significant, further verifying that the amount of leaf tissue removed did not affect the intensity of interspecific competition.

Both intra- and interspecific competition adversely affected phytophagous insects (Fig. 3). There was little evidence, however, that the magnitude of interspecific competition differed from that of intraspecific competition (Fig. 3), including effects on survival ($Q_B = 0.93$, $P = 0.3339$), body size ($Q_B = 1.49$, $P = 0.2224$), oviposition preference ($Q_B = 0.14$, $P = 0.7030$), emigration ($Q_B = 2.62$, $P = 0.1056$), growth rate ($Q_B = 1.96$, $P = 0.1619$), fecundity ($Q_B = 0.47$, $P = 0.4940$), and the composite response ($Q_B = 3.12$, $P = 0.0774$). Although for every response variable there was a trend for the conspecific effect size to be greater than the associated heterospecific interaction, none of these differences was significant.

The phylogenetic similarity between competing species was a poor predictor of the strength of interactions among chewing insects (Fig. 4a; $Q_B = 4.18$, $P = 0.2417$). Competition was weaker between congeners than between more distantly related chewers. This finding is contrary to the expectation of traditional competition theory. Sap-feeding insects, however, provided support for theoretical expectations; phylogenetic relationship influenced the strength of their interactions (Fig. 4b; $Q_B = 41.34$, $P < 0.0001$). This effect was driven by congeners, whose effect size was $\sim 4\times$ greater than more distantly related species.

Generally, there was no difference in the strength of interactions occurring within vs. between feeding guilds (Fig. 5). This was true when assessed for abundance ($Q_B = 0.04$, $P = 0.8477$), development time ($Q_B = 0.82$, $P = 0.3652$), oviposition preference ($Q_B = 2.19$, $P = 0.1393$), plant damage ($Q_B = 0.02$, $P = 0.8771$), body size ($Q_B = 0.01$, $P = 0.9424$), survival ($Q_B = 0.18$, $P = 0.6742$) and the composite response ($Q_B = 0.74$, $P = 0.3885$). Relative growth rate ($Q_B = 21.82$, $P < 0.0001$) was affected by within but not between feeding guild interactions. However, we do not consider this to be particularly strong evidence because only six observations were available for estimating the magnitude of interguild effects on RGR.

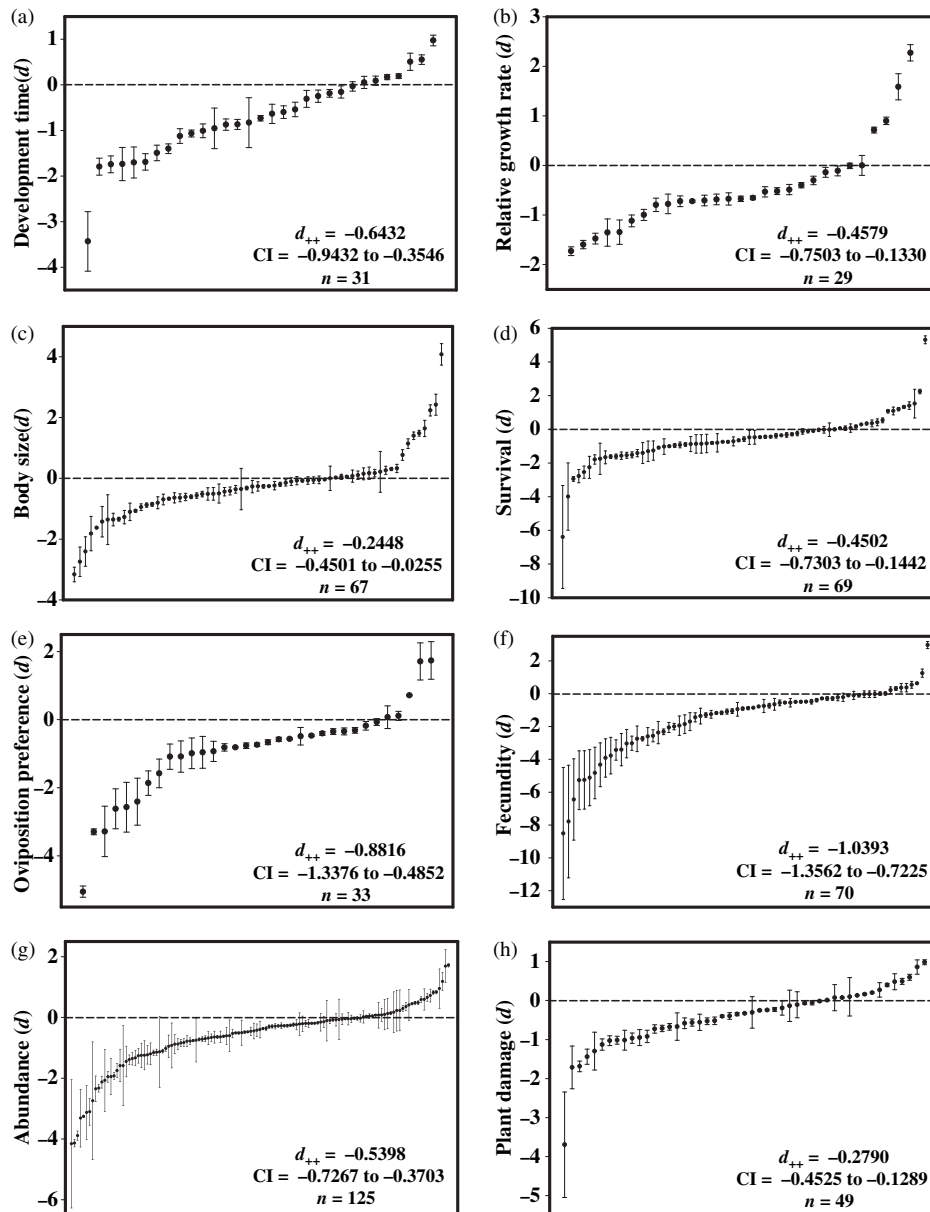


Figure 1 The distribution of effect sizes (Hedges' d) across studies that quantify the impact of interspecific competition on herbivore (a) development time, (b) relative growth rate, (c) body size, (d) survival, (e) oviposition preference, (f) fecundity, (g) abundance, and (h) plant damage. The data are arranged in rank order such that each point represents the effect size and variance for one observation in our dataset. d_{++} = grand mean effect size, CI = 95% bootstrap confidence intervals, n = number of observations.

Spatiotemporal co-occurrence had mixed effects on the strength of interspecific interactions (Fig. 6). For certain response variables there was no effect of separation [growth rate ($Q_B = 1.63$, $P = 0.6526$), survival ($Q_B = 7.41$, $P = 0.0600$)], whereas for other response variables there was [body size ($Q_B = 21.09$, $P = 0.0001$), fecundity ($Q_B = 19.70$, $P = 0.0002$), abundance ($Q_B = 12.52$, $P = 0.0058$), composite response ($Q_B = 25.09$, $P < 0.0001$)]. No consistent patterns emerged from this analysis. In some instances

(e.g. abundance) direct interactions resulted in strong competitive effects, whereas spatiotemporal separation dampened this effect, which is consistent with theoretical expectations. In other cases (e.g. growth rate) the two effects were similar in magnitude, and for two response variables (body size and survival) spatiotemporal separation resulted in stronger competitive interactions than in direct encounters.

For the majority of response variables measured, competition was highly asymmetric (Fig. 7), including effects on

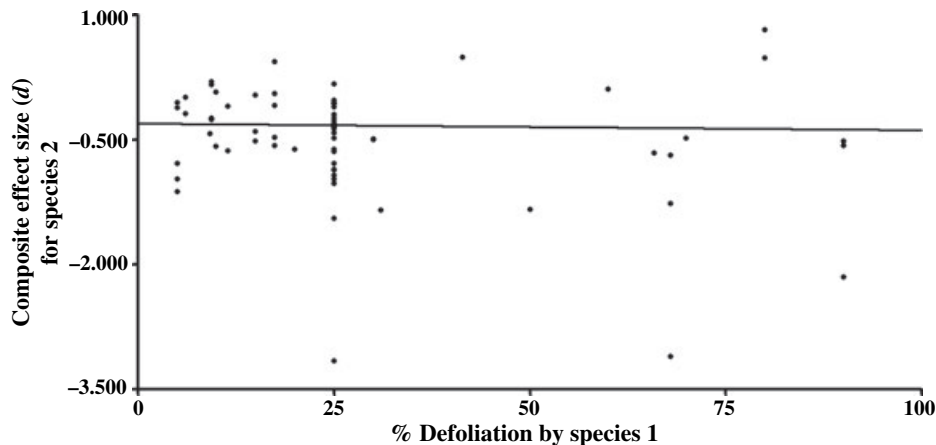


Figure 2 The impact of defoliation intensity by herbivore species 1 on the preference, performance, and/or damage inflicted by herbivore species 2. Theory predicts that interspecific competition is directly proportional to the quantity of resources removed. Therefore, the expectation would be that higher levels of defoliation lead to greater adverse effects on competing species (i.e. a negative relationship between defoliation and effect size).

survival ($Q_B = 8.76$, $P = 0.0031$), fecundity ($Q_B = 7.56$, $P = 0.0060$) and abundance ($Q_B = 9.78$, $P = 0.0018$). Body size ($Q_B = 6.04$, $P = 0.0140$) and growth rate ($Q_B = 2.04$, $P = 0.1527$) were not significant, perhaps due to smaller sample size, but demonstrated strong trends in the same direction as the other response variables. Similarly, the composite response demonstrated a high degree of asymmetry (Fig. 8a; $Q_B = 28.42$, $P < 0.0001$), with the effect of the dominant competitor being $\sim 4\times$ greater than the reciprocal effect from the inferior competitor. Although both direct interactions (Fig. 8b; $Q_B = 11.35$, $P = 0.0007$) and indirect interactions (Fig. 8c; $Q_B = 18.26$, $P < 0.0001$) were asymmetrical, the magnitude of the asymmetry was considerably greater for indirect effects.

DISCUSSION

The overwhelming evidence from this meta-analytical evaluation of interspecific interactions suggests that competition is indeed an important factor influencing the performance and fitness of phytophagous insects. We detected evidence for competition or facilitation occurring in 73% of all pair-wise interactions, which corresponds with frequencies documented in previous reviews on insect herbivore competition (Damman 1993; Denno *et al.* 1995). Moreover, the strength of interactions documented in this study is comparable with other meta-analyses conducted on similar ecological forces (e.g. predation and competition). Halaj & Wise (2001), for example, found that predators reduced the abundance of terrestrial arthropod herbivores ($d = 0.77$). Similarly, Gurevitch *et al.* (1992) reported that competition affected herbivores as a whole ($d = 1.14$), but had very weak effects on terrestrial arthropod herbivores

($d = -0.04$). This earlier assessment of insect herbivore competition by Gurevitch and colleagues, however, was conducted before the recent emergence of studies on indirect interactions and thus suffers from small sample size.

Although the overall effect sizes in our analyses changed depending on the response variable measured (Fig. 1), the magnitude of these effects are within the range documented in the above-cited meta-analyses of predation and competition involving other trophic and taxonomic groups. In fact, we suspect that the effect sizes reported in our study underestimate the ecological significance of competition because of the pervasive impact of facilitation and asymmetry in phytophagous insect communities. Positive interactions (i.e. facilitation) are considered to be common in terrestrial insects (Denno & Kaplan 2007; Marquis & Lill 2007), and are evident in our dataset (Fig. 1; all response variables include multiple effect sizes > 0). Asymmetrical interactions are far more common than symmetrical ones (see 'Symmetry' section below), and the overall impact of the dominant competitor was quite large ($d = -1.1$; see Cohen 1988). The consequence of including facilitation and asymmetry in our assessment is that average effect sizes are diluted throughout and thus provide a conservative estimate of the impact of competition.

Despite empirical support for the overall strength of competition in phytophagous insects, we find very little correspondence with traditional paradigms. Competition is not correlated with levels of defoliation, occurs among distantly related species in different feeding guilds, is not generally dampened by spatial and temporal resource partitioning, and is highly asymmetric.

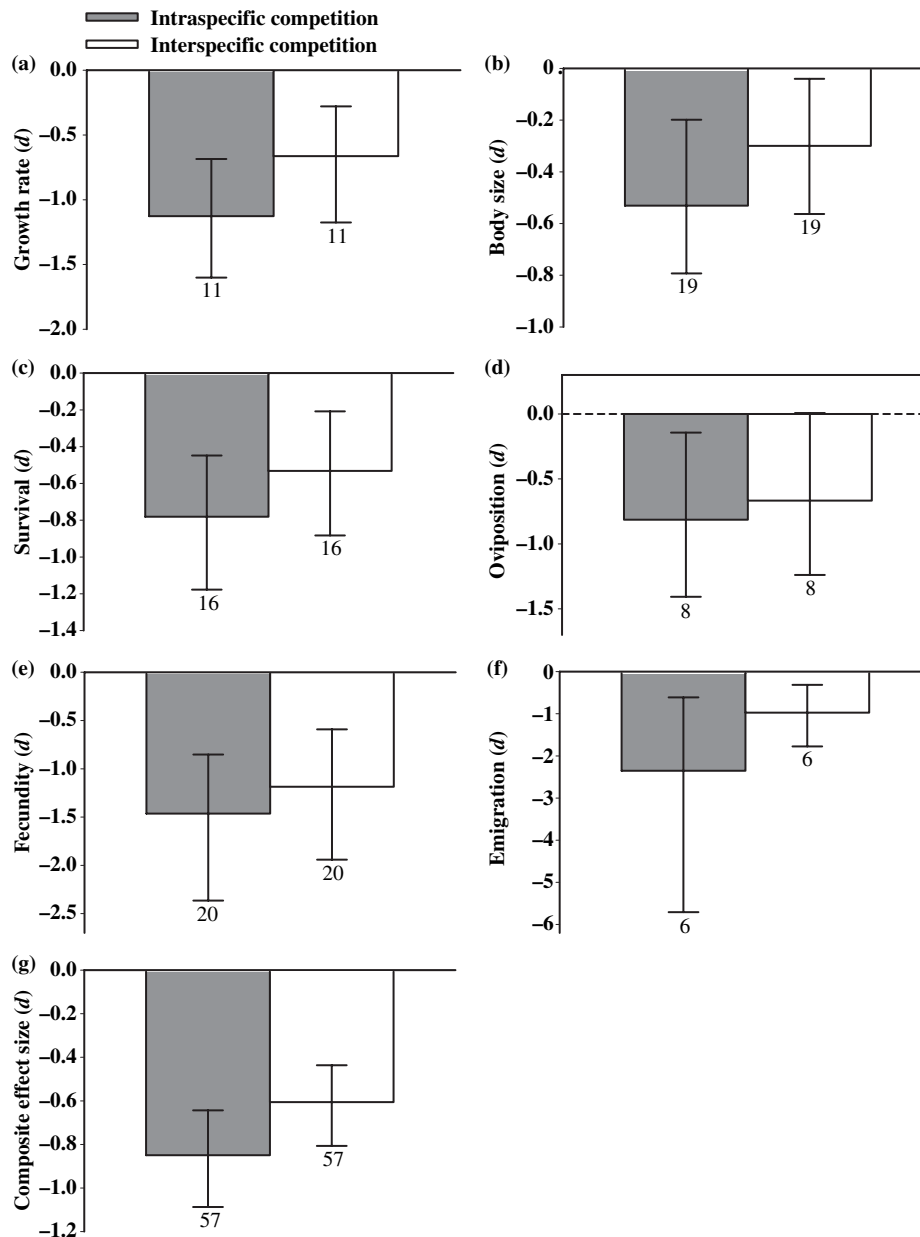


Figure 3 The effects of intra- and interspecific competition on herbivore (a) growth rate, (b) body size, (c) survival, (d) oviposition preference, (e) fecundity, (f) emigration, and (g) composite response. Theory predicts that intraspecific competition will be greater in magnitude than interspecific competition. Because of small sample size, development time and relative growth rate were merged to form the single response variable 'growth rate'. Mean effect sizes are presented with 95% bootstrap confidence intervals, and numbers below error bars are the number of observations per group. None of the comparisons was significant.

Quantity of resources consumed

Exploitative competition occurs when one species consumes and thus reduces the quantity of resources available to competitors (Begon *et al.* 2005). Therefore, the impact of resource removal on potentially competing species should be correlated with the quantity of resources removed (i.e.

intense competition when resource removal is high). In fact, the observation that herbivorous insects typically consume a small fraction of potentially available plant foliage has long been used to justify the stance that competition is rare among insects (Hairston *et al.* 1960). However, we found no relationship between defoliation (%) and the strength of interspecific competition (Fig. 2), supporting the notion that

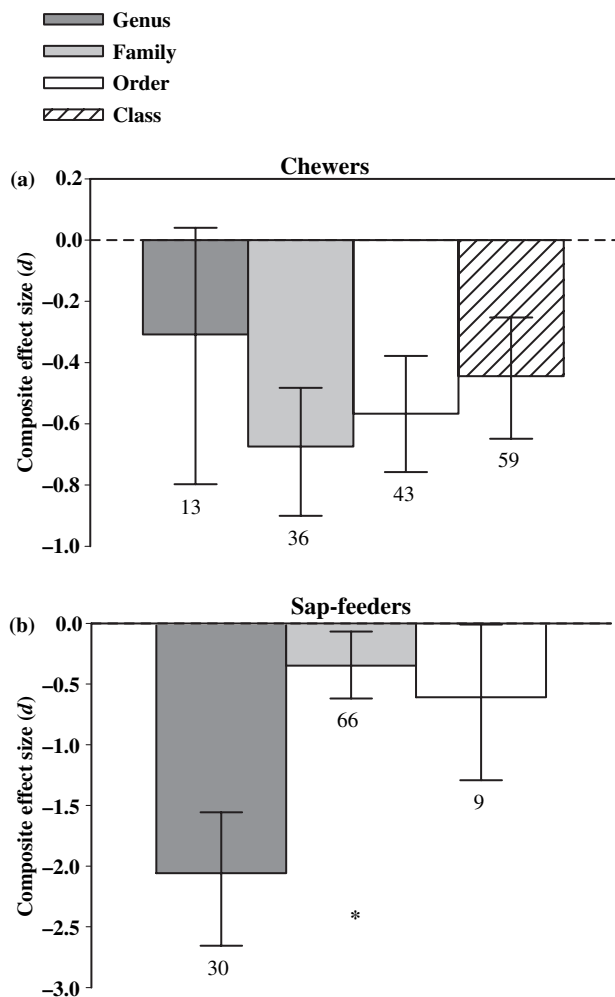


Figure 4 Consequences of phylogenetic relatedness among interspecific competitors on the strength of competitive interactions. Separate analyses were conducted for interactions occurring within (a) chewing, and (b) sap-feeding guilds. Genus, family, order, and class represent the lowest possible shared taxonomic classification among competitors. For example, the group ‘genus’ consists of competing congeneric pairs (e.g. *Prokelisia dolus* and *Prokelisia marginata*). Similarly, ‘family’ signifies competitors in the same family, but not genus (e.g. *Myzus persicae* and *Aphis gossypii*; both in the family Aphididae, but different genera). We could not compare cross-order interactions (‘class’ grouping) for sap-feeders because all published accounts were within the order Hemiptera. Theory predicts that closely related species will compete more intensely than distantly related species. As a result, effect sizes should be greatest among congeners and weakest in the grouping ‘class’ (cross-order interactions). Mean effect sizes are presented with 95% bootstrap confidence intervals, and numbers below error bars are the number of observations per group. *Significant difference ($P < 0.01$) between groups.

even small amounts of damage can induce systemic defenses with important ecological effects (Denno & Kaplan 2007). This pattern prevailed on both woody and herbaceous

plants suggesting that the consequences of minor herbivory for heterospecific herbivores can be severe independent of plant growth form.

This result is not simply an artifact of combining multiple dissimilar plant systems. Induced resistance to beet army-worm caterpillars (*Spodoptera exigua*) on tomato, for example, occurs at very low levels of defoliation, and the magnitude of this effect does not change as total leaf area removal varies from $< 1\%$ to 10% (Stout & Duffey 1996; but see Table 4.5 in Karban & Baldwin 1997 for cases where damage intensity is correlated with induced resistance). Other studies have also documented strong interspecific effects at defoliation levels where the quantity of available leaf tissue is clearly not limiting for herbivores (e.g. Harrison & Karban 1986; Agrawal 1999, 2000; Wise & Weinberg 2002; Van Zandt & Agrawal 2004a,b; Viswanathan *et al.* 2005).

An additional factor that confounds the relationship between resource removal and competition is interspecific facilitation. High levels of defoliation can elicit a *positive* response in subsequent herbivores by weakening plant defense systems (e.g. resin flow in conifers), or stimulating a re-flush of young, nitrogen-rich leaves (Rockwood 1974; Potter & Redmond 1989; Rieske & Raffa 1998; Wallin & Raffa 2001).

Overall, these results make it very difficult to predict competitive outcomes based purely on the amount of leaf tissue consumed, and consequently herbivorous insects may not fit the traditional paradigm for exploitative interactions. Thus, in light of inducible plant defenses, the theoretical basis underlying the argument that ‘herbivores are seldom food-limited...and therefore are not likely to compete for common resources’ (Hairston *et al.* 1960) appears seriously flawed.

Phylogenetic similarity

The hypothesis that closely related species compete more intensely than distantly related ones has long been considered a truism in ecology. Even Darwin predicted that ‘the most closely allied forms – varieties of the same species, and species of the same genus or related genera – which, from having nearly the same structure, constitution and habits, generally come into the severest competition with each other’ (Darwin 1859). Therefore, the relationship between phylogenetic similarity and interaction strength is a fundamental tenet deeply embedded in competition theory. We tested the impact of phylogenetic similarity at two different levels: (i) intra- vs. interspecific competition and (ii) taxonomic relatedness among interspecific competitors.

Previous competition reviews provide mixed support for competition occurring within vs. between species (Connell 1983; Gurevitch *et al.* 1992; Denno *et al.* 1995). Although we

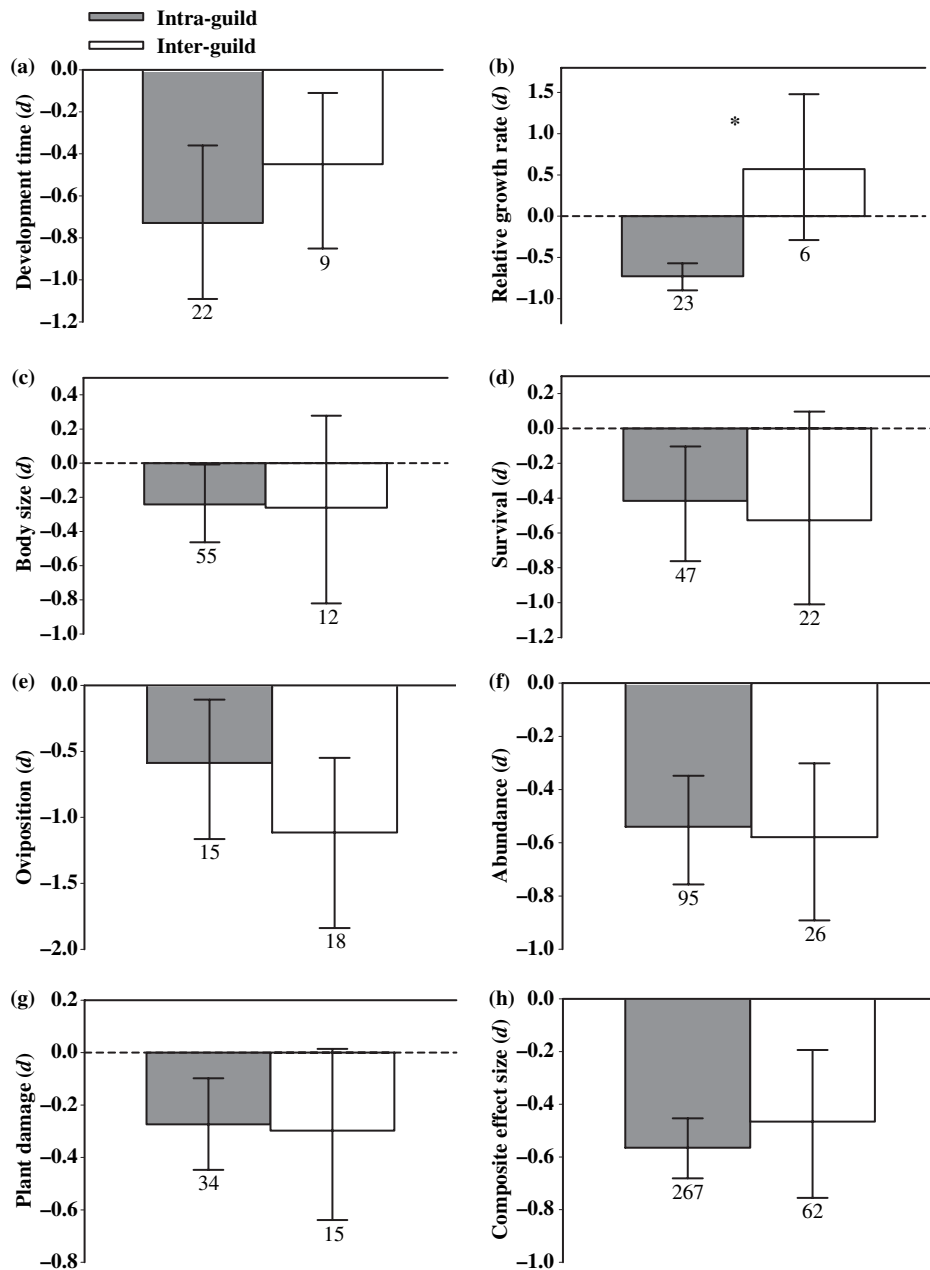


Figure 5 The effects of within and across feeding guild interactions on herbivore (a) development time, (b) relative growth rate, (c) body size, (d) survival, (e) oviposition preference, (f) abundance, (g) plant damage, and (h) composite response. Intraguild interactions are those occurring between herbivores in the same feeding guild (e.g. chewer on chewer, or sap-feeder on sap-feeder). Interguild interactions occur among herbivores in different feeding guilds (e.g. chewer on sap-feeder, or sap-feeder on chewer). Theory predicts that within guild competition will be stronger than competition between guilds. Mean effect sizes are presented with 95% bootstrap confidence intervals, and numbers below error bars are the number of observations per group. *Significant difference ($P < 0.01$) between groups.

find trends in all of our response variables for conspecifics to compete more intensely than heterospecifics, none of these differences were statistically significant indicating that intra- and interspecific competitive effects are comparable in magnitude (Fig. 3). Similarly, taxonomic relatedness had

mixed effects on interspecific competitors. Chewing insects do not conform to theoretical expectations (Fig. 4a), whereas sap-feeders provide some support with congeners competing more intensely than distantly related species pairs (Fig. 4b). As a whole, the evidence in our dataset for

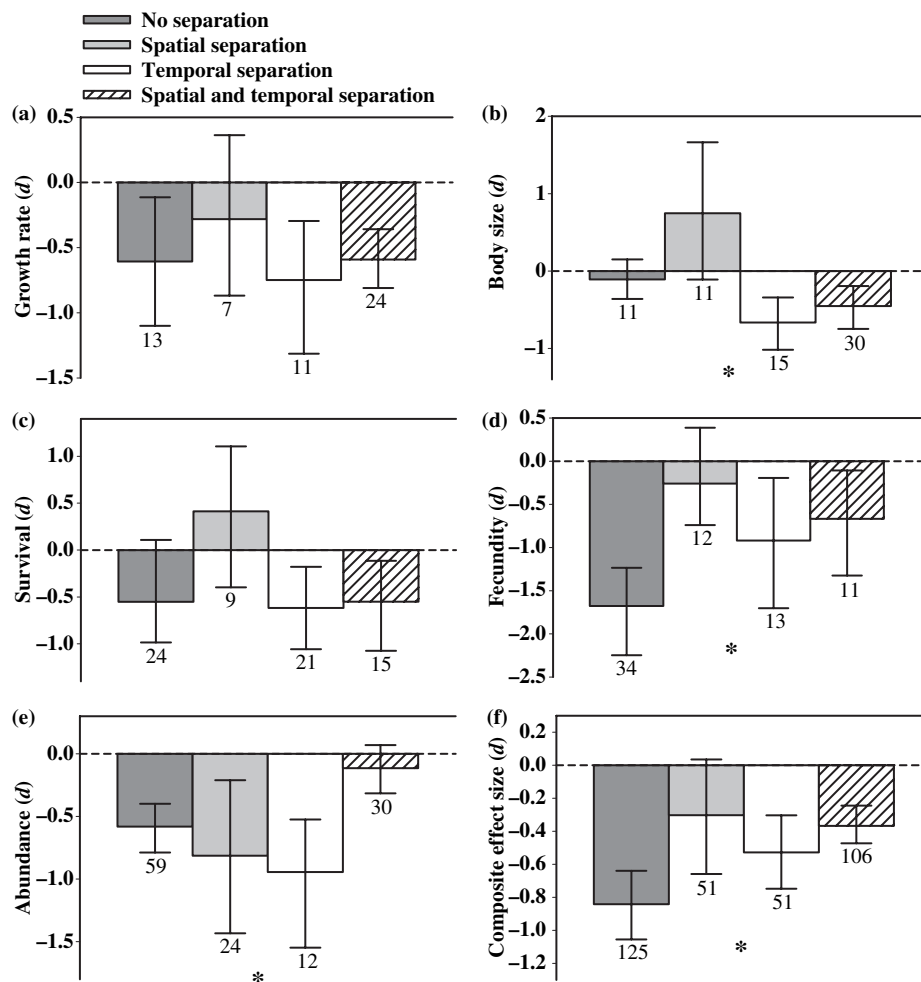


Figure 6 The impact of spatial and/or temporal separation on the strength of interspecific competition, including effects on herbivore (a) growth rate, (b) body size, (c) survival, (d) fecundity, (e) abundance, and (f) composite response. Interactions were classified as occurring among herbivores that are (i) not separated from one another, (ii) spatially separated (e.g. leaf- and root-feeders) but occur on the plant at the same time, (iii) temporally separated (e.g. early- and late-season species) but share the same plant part, and (iv) spatially and temporally separated. Theory predicts that spatiotemporal co-occurrence will promote more intense competition. Because of small sample size, development time and relative growth rate were merged to form the single response variable 'growth rate'. Mean effect sizes are presented with 95% bootstrap confidence intervals, and numbers below error bars are the number of observations per group. *Significant difference ($P < 0.01$) between groups.

phylogenetic similarity promoting competitive interactions is relatively weak. Rather, our findings support the more recent view that competition frequently occurs among divergent taxa (Hochberg & Lawton 1990), including distantly related herbivorous insects (Van Zandt & Agrawal 2004b; Denno & Kaplan 2007).

We suspect that the lack of correspondence with traditional paradigms in this instance stems from the fact that, historically, competition theory has emphasized direct interactions, whereas many documented cases of competition in phytophagous insects are indirect and mediated by plants and/or natural enemies (Damman 1993). As a result,

the nature of the indirect effect should be more important than the degree of phylogenetic similarity. For instance, many herbivore-induced plant allelochemicals (e.g. nicotine) have broad-spectrum efficacy and thus do not discriminate among taxa (Karban & Baldwin 1997). Consequently, one herbivore can induce plant defenses that impact other herbivores sharing the host-plant, independent of their phylogenetic relationship. Plant damage by sap-feeding whiteflies, for instance, elicits elevated expression of defensive proteins that negatively affect leaf-chewing caterpillars (Inbar *et al.* 1999). In a similar manner, enemy-mediated interactions (i.e. apparent competition) can link

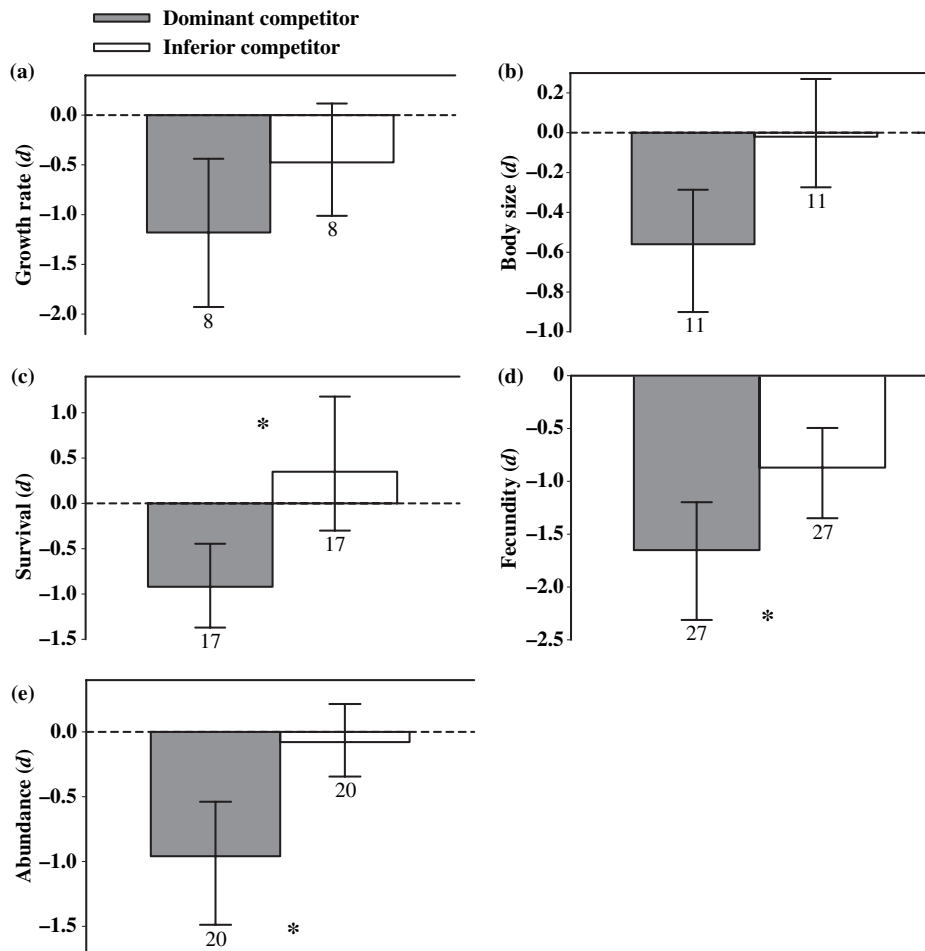


Figure 7 The symmetry of reciprocal pair-wise interactions between competing herbivores. The effects of dominant and inferior competitors were reported on herbivore (a) growth rate, (b) body size, (c) survival, (d) fecundity, and (e) abundance. Reciprocal interactions (i.e. effects of sp. 1 on 2, and sp. 2 on 1) were paired and the larger of the two effect sizes was used to define the dominant competitor. The smaller effect size defined the inferior competitor. If interactions are symmetrical, as predicted by competition theory, then these two groups should be equal in magnitude. Because of small sample size, development time and relative growth rate were merged to form the single response variable 'growth rate'. Mean effect sizes are presented with 95% bootstrap confidence intervals, and numbers below error bars are the number of observations per group. *Significant difference ($P < 0.01$) between groups.

distantly related herbivores when the shared enemy is a polyphagous predator that indiscriminately attacks prey. Cotton aphids, for example, strongly attract aggressive fire ants onto plant foliage and these ants subsequently attack co-occurring herbivores, including caterpillars and other distantly related taxonomic groups of insects (Kaplan & Eubanks 2005).

Intra- vs. interguild interactions

Because herbivores in the same feeding guild consume plants in a similar manner they are considered more likely to compete with one another than herbivores in discrepant feeding guilds. However, early experimental field studies on

insect competition contradict this hypothesis (Faeth 1986; Karban 1986, 1989). Unlike Denno *et al.* (1995) who found support for guild differences diminishing competition, we find no evidence that the strength of intraguild interactions (chewer/chewer, sap-feeder/sap-feeder) differs from that of interguild interactions (chewer/sap-feeder) (Fig. 5). Because we grouped herbivores according to major feeding guilds (e.g. chewer or sap-feeder), rather than dividing them into sub-guilds (e.g. phloem-feeder, leaf-miner, gall-former, etc.), our results might underestimate the potential for guild differentiation to mediate competitive strength. For example, one might expect that concealed feeders (e.g. leaf-miners) confined to very specific resources compete more intensely than free-living chewers (Denno *et al.* 1995).

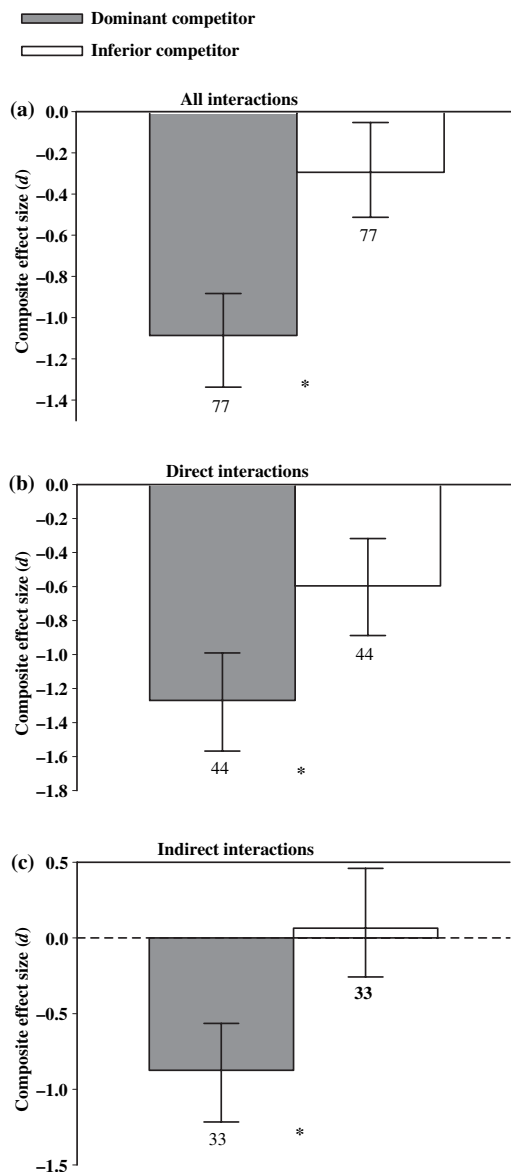


Figure 8 The symmetry of reciprocal pair-wise interactions between competing herbivores. The effects of dominant and inferior competitors were reported on herbivore composite response for (a) all interactions, (b) direct interactions, and (c) indirect interactions. Reciprocal interactions (i.e. effects of sp. 1 on 2, and sp. 2 on 1) were paired and the larger of the two effect sizes was used to define the dominant competitor. The smaller effect size defined the inferior competitor. If interactions are symmetrical, as predicted by competition theory, then these two groups should be equal in magnitude. Mean effect sizes are presented with 95% bootstrap confidence intervals, and numbers below error bars are the number of observations per group. *Significant difference ($P < 0.01$) between groups.

Unfortunately, due to lack of adequate replication, the analysis of sub-guild interactions could not be performed. Nonetheless, interguild interactions are now

well-documented in a variety of systems (Karban 1986, 1989; Inbar *et al.* 1999; Kessler & Baldwin 2004; Van Zandt & Agrawal 2004b; Lynch *et al.* 2006; Kaplan *et al.* 2007). Future studies that quantify the mechanistic underpinnings of plant responses to herbivores (especially sap-feeding insects), including secondary metabolite expression and source-sink dynamics, will greatly contribute to our understanding of when and why interguild interactions occur (Karban & Baldwin 1997; Denno & Kaplan 2007).

Spatial and temporal resource partitioning

When two herbivores that share a common host-plant co-occur in time and space, competition is predicted to be intense. Partitioning the resource, however, by emerging and feeding at different times of the growing season and/or utilizing different parts of the plant is thought to differentiate niches and thus diminish competition (Schoener 1974; Connell 1980). Based on their earlier review of the literature, Denno *et al.* (1995) concluded that resource partitioning dampens, but does not preclude competition between temporally and spatially separated species. Our data tend to support this view, although the results were mixed and depended on which response variables were measured (Fig. 6). The ecological significance of competition between spatially and temporally separated species will ultimately be determined by the spatial extent and temporal persistence of indirect plant- and enemy-mediated effects.

Herbivore-induced plant defenses are generally considered to be strongest at the site of attack soon after damage occurs, and these effects wane with time and space (Karban & Baldwin 1997). Plant induction, however, can nonetheless link spatially and temporally separated species. For example, the phytophagous mirid bug, *Tupiocoris notatus*, induces resistance to hornworm caterpillars, *Manduca quinquemaculata*, on wild tobacco, and this effect is as strong or stronger when caterpillars are fed systemic, undamaged leaves compared with locally damaged leaves (Kessler & Baldwin 2004). Similar results were found for the impact of gypsy moth, *Lymantria dispar*, defoliation on swallowtail caterpillars, *Papilio canadensis* (Redman & Scriber 2000). Induced defenses can also persist long after damage to the plant occurs. Several studies have found poor correlations between time from induction and the strength of induced resistance (Gibberd *et al.* 1988; Stout & Duffey 1996); in these cases the effects of induced resistance persist for at least 2–3 weeks after damage. Similarly, interyear carryover effects from outbreak defoliators (e.g. DIR – delayed induced resistance) allow for plants to mediate interactions between herbivores across different growing seasons (Kaitaniemi *et al.* 1998, 1999).

Natural enemies can also extend herbivore competition across time and space, although their spatiotemporal effects are likely to differ from plants. Because many natural enemies actively search for prey, we suspect that their temporal persistence will be less than induced plant defenses. In other words, the impact of early-season herbivores on late-season herbivores via natural enemies may be weak because predators and parasitoids will likely emigrate in search of alternative food after their focal prey disappears. Unlike induced defenses, however, natural enemies can mediate competition between herbivores on different plants, and therefore their spatial reach is far greater than induced defenses (but see Karban *et al.* 2006; Baldwin *et al.* 2006 for evidence of interplant communication via damage-induced volatiles). The invasion of soybean aphids (*Aphis glycines*) in the Midwestern United States, for instance, has increased the abundance of predaceous coccinellid beetles that migrate into alfalfa fields and severely reduce pea aphid (*Acyrtosiphon pisum*) densities (Harvey 2007). As a result, soybean aphids strongly 'compete' with pea aphids, even though neither feeds on the same host-plant and their respective hosts occur in different agricultural fields that are separated by great distances.

Symmetry

Historically, interspecific competition is thought to entail a reciprocal struggle for resources, although most prior reviews do not support this prediction (Lawton & Hassell 1981; Connell 1983; Schoener 1983; Strong *et al.* 1984; Denno *et al.* 1995; Denno & Kaplan 2007). In fact, the lack of symmetry in interspecific interactions is one of the few generalities that emerge and appear to remain consistent across trophic levels and taxonomic groups. Our data strongly support this conclusion for phytophagous insects (Figs 7 and 8a). Moreover, by grouping effect sizes according to the dominant and inferior competitors for each interspecific pair we could quantify the degree of reciprocal effects and thus assess the symmetry of interactions. In this case, the impact of the dominant competitor was 4× greater than the reciprocal effect of the inferior species. Importantly, the inferior competitor had a significant, albeit weak, reciprocal effect in direct interactions (Fig. 8b), but its impact was non-significant when assessing indirect (mostly plant-mediated) interactions (Fig. 8c). This pattern suggests that asymmetry is far more pronounced with indirect effects and offers strong support for the view that indirect interactions violate the traditional dogma of competition theory.

The mechanisms underlying competitive dominance, and thus asymmetrical interactions, are diverse (e.g. aggregation, dispersal, tolerance of allelochemistry; see Denno & Kaplan 2007). For instance, early-season exploitation of host-plants

creates a condition in which initial colonizers affect subsequent herbivores, but reciprocal effects of late-season feeders on early-season herbivores are unlikely. Thus, inherent differences in the phenology of insects on plants in seasonal environments promote asymmetry. Notably, such cases of temporal displacement between two herbivores in which only one-way effects were assessed were not included in our assessment of reciprocal interactions, and thus our finding of asymmetry was not over inflated for this reason.

In other instances, however, the mechanisms generating asymmetry are far more idiosyncratic and unpredictable. For example, two phytophagous beetles (*Psylliodes affinis* and *Plagiometriona clavata*) commonly attack the nightshade *Solanum dulcamara*; in this system, *P. affinis* has strong plant-mediated effects on *P. clavata*, but *P. clavata* has no reciprocal impact on *P. affinis* (Viswanathan *et al.* 2005). In this example, both herbivores are beetles in the family Chrysomelidae and experiments controlled for the quantity of leaf tissue damaged. Therefore, the asymmetry in this interaction is likely due to interspecific differences in feeding patterns, salivary constituents, or other undetermined factors. Similarly, gall-forming herbivores can dominate interactions with other sap-feeding insects by inducing stronger metabolic sinks as a consequence of positioning their gall basal to potentially competing species on the same leaf (Inbar *et al.* 1995).

A more holistic perspective on interspecific competition: integrating the old with the new

The emergence of non-traditional mechanisms promoting competition in modern ecology is apparent, not only in phytophagous insects, but in a wide range of taxa and ecosystems. The mechanisms underlying competition in plant assemblages, for example, are being challenged by facilitation (Stachowicz 2001; Bruno *et al.* 2003), and indirect interactions mediated by herbivores (i.e. associational resistance and susceptibility; Rand 2003). Analogous processes have also recently been uncovered and emphasized in marine (Long *et al.* 2007) and mammalian systems (Roemer *et al.* 2002). Thus, given the ubiquitous presence of non-traditional forms of competition in phytophagous insects, as well as other animal and plant groups, defining a new paradigm for interspecific competition should be a priority for the fields of population and community ecology (e.g. Bruno *et al.* 2003).

Based on our analyses, current competition theory inadequately predicts the nature of interactions occurring in herbivorous insects; virtually every fundamental paradigm that we tested was violated to some degree, suggesting a poor concordance between theory and empirical patterns. Although advancement in science typically occurs when traditional theories are restructured or otherwise modified to

account for newer findings, the extreme disparity between theory and empirical results for phytophagous insects leads us to question if and when the historical perspective on competition applies. More specifically, the conceptual basis for traditional, niche-based competition theory is simply too restrictive to adequately account for current findings, at least those involving insect herbivores. Lawton & Strong (1981) expressed a similar concern years ago with regard to traditional competition and niche theory and their ability to predict interactions among insect herbivores.

Indirect herbivore interactions via plants and enemies are likely to underlie much of the discrepancy between theory and pattern. Until recently, most ecology texts emphasized interference and exploitative interactions as the two mechanisms driving competition. Our dataset provides weak support for the overall prevalence of these two mechanisms occurring in phytophagous insect communities (Fig. 9). Alternatively, indirect interactions provide the vast majority of evidence for interspecific herbivore interactions (> 65% of all observations in our dataset), particularly those involving plants. The frequency of enemy-mediated interactions, however, is likely to be highly underestimated in our dataset because the response variables used in many studies on apparent competition (e.g. % parasitism) could not be integrated into our analyses. Similarly, facilitation, although accounting for > 15% of all interactions, may be underestimated because many cases of positive interspecific effects quantify diversity rather than herbivore preference or performance (e.g. Lill & Marquis 2003; Marquis & Lill

2007). Thus, despite the fact that indirect interactions and facilitation are already well-represented in our dataset, their frequencies provide a conservative estimate of their prevalence in insect communities.

An additional component of indirect plant- and enemy-mediated interactions is that they often impact the entire community of herbivores, leading to more diffuse interspecific effects (Thaler *et al.* 2001; Van Zandt & Agrawal 2004b; Agrawal 2005; Kaplan & Eubanks 2005; Viswanathan *et al.* 2005), in contrast with the traditional focus on pair-wise species interactions. Moreover, natural enemies can exacerbate plant-mediated effects between herbivores, a community-level interaction that remains unexplored in most systems. For example, previous feeding by potato leafhoppers (*Empoasca fabae*) results in adverse plant-mediated effects on other herbivores (e.g. slow growth), which in turn dramatically increases their risk of predation (Kaplan *et al.* 2007). As a result, the new paradigm for interspecific competition must take a community-wide perspective that recognizes positive as well as negative interactions that propagate from both the bottom and top of trophic webs. Furthermore, these interspecific effects are predicted to be highly asymmetric, occur at relatively low herbivore densities, and among divergent taxa that feed at different times and on different plant tissues. A major consequence of this approach is that niche overlap, at least as historically defined, will play a decreasingly important role. Although this paradigm is not likely to be what Darwin and other early ecologists had envisioned in the development of

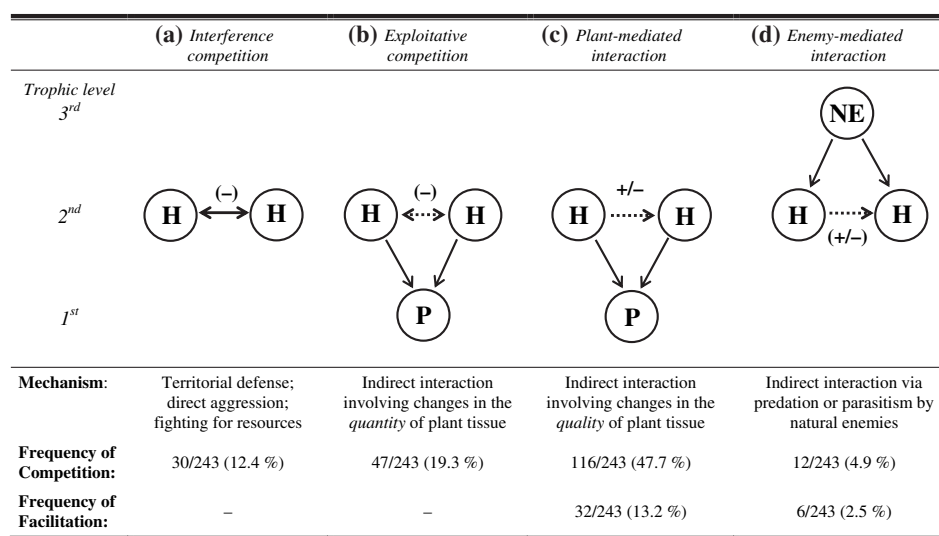


Figure 9 Potential mechanisms underlying competitive and facilitative interactions between herbivores, including (a) interference competition, (b) exploitative competition, (c) plant-mediated interactions, and (d) enemy-mediated interactions. Frequencies represent the proportion of all interactions in our dataset that correspond to each category (i.e. interference competition = 12.4% = 30 observations of interference/243 total observations of significant interspecific interactions). Direct effects are indicated by solid lines, whereas indirect effects are signified by dashed lines. NE, natural enemies; H, herbivores; P, plants, -, competition, +, facilitation.

competition theory, it should be central to any current perspective on interspecific interactions involving herbivorous insects, and perhaps other trophic and taxonomic groups.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Meta-analysis literature.

Appendix S2 Meta-analysis effect size table.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2007.01093.x>.

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