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LETTER

When do herbivorous insects compete? A phylogenetic meta-analysis

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Abstract

When herbivorous insects interact, they can increase or decrease each other's fitness. As it stands, we know little of what causes this variation. Classic competition theory predicts that competition will increase with niche overlap and population density. And classic hypotheses of herbivorous insect diversification predict that diet specialists will be superior competitors to generalists. Here, we test these predictions using phylogenetic meta-analysis. We estimate the effects of diet breadth, population density and proxies of niche overlap: phylogenetic relatedness, physical proximity and feeding-guild membership. As predicted, we find that competition between herbivorous insects increases with population density as well as phylogenetic and physical proximity. Contrary to predictions, competition tends to be stronger between than within feeding guilds and affects specialists as much as generalists. This is the first statistical evidence that niche overlap increases competition between herbivorous insects. However, niche overlap is not everything; complex feeding guild effects indicate important indirect interactions.

Keywords

Competition, enemy-mediated, indirect competition, plant-mediated, tri-trophic interactions.

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INTRODUCTION

Herbivorous insects form a major component of terrestrial communities and account for ~ 1/3 of all described species (Grimaldi & Engel 2005). Community assembly and species diversification are thought to depend on how interacting species affect one another's fitness (Levins 1968). For herbivorous insects such effects can be variable, ranging from fierce competition to facilitation. We currently know little of what causes this variation. Knowing more could bring us to a deeper understanding of how speciation happens (Alatalo *et al.* 2018) and of how communities are structured.

When should we expect herbivorous insects to compete? According to classic competition theory, competition should increase with niche overlap and population density, that is, when more individuals vie for the same resources (Levins 1968). But it is not clear how useful this theory is for herbivorous insects. One problem is that most herbivorous insects tend to occur at low density. This rarity inspired the Green World Hypothesis (Hairston *et al.* 1960): Herbivorous insect populations are under such strong natural enemy pressure that they do not compete for host plant resources. Thus, most plant parts go uneaten and the world is green. Of course, this takes a simplistic view of how plants interact with their insect herbivores. For herbivorous insects, plants are more than food; they can provide refuge from natural enemies and a place to interact with mutualists. Moreover, not all plant tissues are equally nutritious, and they can vary in their state of defensiveness against herbivory. This means that competition between herbivorous insects can be indirect, as they induce host–plant defenses (Price *et al.* 2011), attract natural enemies (Faeth 1986; Mooney *et al.* 2012) and distract mutualists (Styrsky & Eubanks 2007). If the interactions between herbivorous insects are mostly indirect, classic competition theory predictions might not apply.

Decades of research (Denno *et al.* 1995; Kaplan & Denno 2007; Radville *et al.* 2014) have shown us that – at least in experiments – competition between herbivorous insects is common, even if two individuals are never in physical contact or even on the same host at the same time (e.g. Ammunét *et al.* 2010; Anderson *et al.* 2011; Van Dam & Heil 2011). In the current view, the fitness effects of herbivorous insect interactions do not appear to depend much on niche overlap (Kaplan & Denno 2007). Thus, classic competition theory seems of little use. However, this view could be warped by two major biases. First, until recently, researchers have had little ability to account for the phylogenetic non-independence of their fitness measures: similarity in competitive ability between two species could be due to similar values for a predictor variable such as trophic mode, or it could be due to shared ancestry. Second, researchers have tended not to control for density when assaying the fitness effects of herbivorous insect interactions. Both biases, phylogeny and density, can be addressed with current meta-analytic approaches.

Predictions about when herbivorous insects compete can also be drawn from classic hypotheses about what drives their speciation. Most herbivorous insects are host-use specialists, and this specificity is commonly assumed to be part of why they are so species rich. But the adaptiveness of specificity is anything but clear (see reviews by Futuyma & Moreno 1988; Forister *et al.* 2012). Few host-use trade-offs have been identified that would select against broad diets (e.g. Agosta & Klemens 2008). But trade-offs in competitive ability *per se* have yet to be tested; perhaps specialists predominate because they are better indirect competitors.

Here, we use phylogeny-informed meta-analysis to address three main questions. (1) On average, do herbivorous insects

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compete? (2) Does classic competition theory predict the fitness effects of an interaction? (3) Can we predict the outcome of interspecific interactions on the basis of a species' diet breadth? Answers to these questions will advance our understanding of herbivorous insect community assembly and species diversification.

METHODS

Data

To assemble a set of relevant and comparable studies, we began with those used by Kaplan & Denno (2007). We then extended that set to include another decade of empirical research, first looking at studies that cited Kaplan & Denno (2007). Literature searches were conducted from 5 to 15 December 2017. We conducted Google Scholar searches for the following terms: 'interspecific competition insects', 'insect interaction', 'plant-mediated interactions insects', 'enemy-mediated interactions insects', and 'apparent competition insects'. These searches yielded > 3 000 000 studies, but we only reviewed the first thousand results for each search term. As we approached that point, studies were largely repeats of previous hits, not peer-reviewed, or did not examine the effects of herbivorous insect interactions on their fitness.

Literature searches were conducted from 5 to 15 December 2017. Most studies were not suitable for inclusion in our meta-analysis. To be included, a study needed to satisfy five criteria: it must (1) have been published in a peer-reviewed journal; (2) examine the interaction between two or more species of herbivorous insects; (3) unambiguously identify the focal species, (4) measure proxies of fitness of the focal species, and (5) provide effect means, variances and sample sizes. Exceptions to the last criterion were made for studies that reported results as population proportions. Sixty-four studies met these criteria and were added to the core set of studies examined by Kaplan & Denno (2007). However, the same criteria also required us to remove 46 of the studies used by Kaplan & Denno (2007), most often because they did not unambiguously identify the focal species or did not provide treatment means, sample sizes and variances. In the end, we examined a total of 167 studies that included 1641 effect sizes. A total of five insect orders and 179 species were represented after standardising scientific names using the Global Names Resolver (https://resolver.globalnames.org/, last accessed 12 July 2018). A list of the studies used in our analysis and a more detailed view of how the studies were chosen is included in Supporting Information S1 and S2, respectively.

Whenever possible, treatment means, variances, and sample sizes were taken directly from tables provided in publications. Otherwise, we extracted these values from figures using WebPlotDigitizer (Rohatgi 2018). To make effect sizes comparable across studies, we converted effect size means into Hedge's *g*, which scales mean differences across experimental treatments to unit variance and weights variances by sample size (Hedges 1981). Note that for Hedge's *g*, the rule of thumb is that effects ~ 0.3 are considered weak, ~ 0.5 are moderate, and > 0.7 are strong (Cohen 1988). Calculations were performed using the *metafor* package (Viechtbauer 2010) in R (v.3.2.1; R Core Team 2018). As mentioned above, most of the analysed effects were expressed as group means and variances, but some were expressed as the proportion of each of two possible outcomes in an experiment (for example, the proportion of insects choosing to settle on one of two hosts). In these cases, we needed to first calculate an effect size as a log odds ratio, and then convert the log odds ratios to Hedge's *g*. The data are provided in Supporting Information S3.

Model parameterisation

Response variables – measures of fitness changes

Studies of herbivorous insect interactions have measured fitness changes with a variety of proxies, that is, fitness components (definitions of these proxies are given in Table 1.) We analysed each of these fitness components individually and in composite, in which case effect sizes from all component types were pooled and weighted equally. Below, we focus on models of composite fitness and models of abundance, which is the most commonly measured fitness component, and the one that probably best encapsulates fitness overall. Negative effect sizes indicate competition, and positive effect sizes indicate facilitation.

Fixed effects – predictors of fitness changes

We first estimated the average impact of insect interaction on each fitness component by fitting linear models in which the intercept was the only fixed effect. We then attempted to explain the variation in how herbivorous insect interactions affected their fitness by considering models with several potential explanatory variables: (1) *Within vs. between species* was a binary variable, distinguishing between intraspecific and interspecific interactions. (2) *Population density* was a binary

Table 1 Analysed fitness components

Fitness component	Units	Effect sizes
Abundance	Number of individuals, per treatment, at end of experiment	430
Body size	Total body mass, body length, or length of specific body part (e.g. femur)	314
Development time	Time to develop from one life stage to another, (e.g. from hatching to pupation)	148
Emigration	Proportion of dispersive individuals in population (e.g. number of alates in a population)	48
Fecundity	Number of eggs or egg batches laid	269
Feeding preference	Proportion of insects that feed on particular host resource in two-choice trial	19
Oviposition	Proportion of insects that oviposit on particular host resource in two-choice trial	38
Relative growth rate (RGR)	Change in body size over time	79
Survival	Proportion of population surviving	271
Others	Fitness components that did not fit into any of these categories	30

Across published studies, changes in fitness were measured with nine variables, referred to here as fitness components. The last column gives the number of effect size for each component type.

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variable, distinguishing between experiments in which population densities were the same in control and treatment groups from experiments in which they were higher in treatments. It would have been preferable to parameterize the absolute density of insect populations in each experiment and to directly compare experimental densities to those that are typical in nature. However, insufficient information was available. Note that previous authors have expressed concern that much of the published research comparing intraspecific and interspecific interactions has been biased by ignoring these kinds of density disparities (Connell 1983; Inouye 2001). (3) *Diet breadth* was a continuous variable: a count of known host plant families for an insect species. This information was taken from Hardy *et al.* (2018) (Supporting Information S4). We also examined models in which diet breadth was a binary variable – that distinguished between specialists (one host plant family) and generalists (two or more host plant families). Parameterising diet breadth in this way made no qualitative differences on our inferences (Supporting Information S5); below we discuss only analyses with the continuous diet–breadth predictor. (4) *Phylogenetic distance* was a continuous variable that quantified the evolutionary divergence between a focal and competitor species. It was calculated with the cophenetic function from the R package *ape* (Paradis *et al.* 2004), using a phylogeny estimated from published DNA sequence data (see below for details). (5) *Spatial separation* was a binary variable. Studies were classified as either permitting or forbidding physical contact between the focal and competitor species. We considered physical contact permissible if insects fed on the same host and tissue (e.g. leaves, roots, or stems) unless the experimental design took measures to isolate individuals on the same tissue type. (6) *Temporal separation* was coded as a three-level factor. In the first level, the competitor was introduced at the same time as the focal species. In the second level, the competitor was introduced before and remained after the introduction of the focal species. In the third level, the competitor was introduced and removed before the introduction of the focal species. Significant fitness effects when herbivores are temporally separated indicate important indirect interactions. (7) *Feeding guild* was coded as a factor with three levels: chewers (including leaf and root feeders), sap-feeders, and internal feeders (including gallers, leaf miners, and stem borers). Because the majority of herbivorous insects are chewers, this category was used as the reference in comparison to other guilds. Although it could have helped us understand indirect interactions, we were unable to include a variable indicating whether tri-trophic indirect interactions (via mutualists or natural enemies) could have occurred in an experiment, as too few studies were unambiguously tri-trophic.

Random effects

The covariates in our models do not vary independently. Specific causes of non-independence include the phylogenetic relatedness of focal species, experimental design differences between research groups, and the year a study was published. We sought to account for these sources of non-independence by including them as random variables in our regression models.

To account for non-independence caused by researchers using similar methods, we grouped researchers who had written papers together and included those groups as a random term in all models. (Alternative models with un-grouped studies as random effects yielded similar results.)

We used two approaches to account for phylogenetic relatedness. One set of models specified explicit covariance structures based on estimated phylogenetic relationships among species (see below for details). We refer to these as phylogenetic models. A second set of models approximated phylogenetic relatedness with nested random effects corresponding to three levels of hierarchical classification: genus, family and order. We refer to these as taxonomic models. The phylogenetic models more accurately express evolutionary relationships, but since phylogenetic data were not available for all species, the taxonomic models were more inclusive. Moreover, the phylogenetic and taxonomic models imply distinct evolutionary processes; the phylogenetic models imply that traits evolve gradually, via Brownian motion over phylogenetic branches, whereas the taxonomic models imply a more saltatory process. If fixed effect estimates are consistent across phylogenetic and taxonomic models, it suggests that the results are robust to our assumptions about macro-evolutionary processes.

To estimate a phylogenetic relationship among the studied insect species, we used PyPHLAWD (Smith & Brown 2017) to aggregate and align clusters of published DNA sequence data from three loci (COI, EF-1α, 18S). We then used RaxML v8.1.16 (Stamatakis 2014) to conduct a maximum likelihood (ML) tree search on a concatenation of these loci. For this search, we used the NCBI taxonomy as a topological constraint. In other words, we did not attempt to estimate every phylogenetic relationship from scratch, but rather conducted an analysis to resolve relationships within levels of the taxonomic heirarchy and estimate phylogenetic branch lengths. The tree search consisted of 100 non-parametric bootstrap (BS) replicates under a General Time Reversible model of DNA substitution with CAT-approximated among-site rate heterogeneity. Model parameters were estimated independently from each locus. Then every 5th BS tree was used as the starting tree for more thorough optimisation of the observed data. We scaled the ML tree's branch lengths to time, under an autocorrelated model of among-branch substitution rate variation, using the penalised-likelihood approach implemented in TreePL (Smith & O'Meara 2012). For this step, we used 15 node age calibrations (Supporting Information S6) taken from the TimeTree database of published divergence time estimates (Hedges *et al.* 2006). Each node constraint was a uniform distribution, with the TimeTree age used as a minimum constraint, and a maximum age set to 10 Ma older than the minimum. In the end, we had a time-scaled phylogeny that covered 164 of the 251 species represented in the meta-analysis (Supporting Information S7).

Analysis

We fit mixed effect meta-regression models using the Bayesian approach implemented in the R package MCMCglmm (Hadfield 2010). Each MCMC chain was run for 1 000 000

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iterations with a 500 000 iteration burn-in and a 100-iteration thinning interval. The Geweke diagnostic (Plummer *et al.* 2006) was used to test for convergence; all models were sampled adequately from the stationary distribution. To avoid problems with repeatedly testing, the same data for different effects and to gain a more comprehensive view of how potential predictor variables interact, all fixed effects were included in each model with two exceptions: diet breadth and pairwise phylogenetic distance. Data for these variables were available for only a subset of species. Specifically, inclusion of diet breadth as a covariate would have required us to drop 183 of 1429 effect sizes from the composite fitness taxonomic model and 112 of 1219 effect sizes from the composite fitness phylogenetic model. And inclusion of the phylogenetic distance between focal and competitor species would have required dropping 437 and 227 effect sizes from the taxonomic and phylogenetic models, respectively. Therefore, we excluded these covariates from our main models, and independently estimated their effects on fitness. R code is provided in Supporting Information S8.

To test for publication bias, we used three functions in the R package *metafor*. We first checked a funnel plot for strong asymmetries (Supporting Information S9); it showed a small positive skew, but appeared close to symmetrical. We then performed Egger's regression test (Nakagawa & Santos 2012; Egger *et al.* 2015) and the trim-and-fill test (Duval & Tweedie 2000). Statistical tests for bias were inconsistent; Egger's test indicated that publication bias was significant ($z = 9.17$, $P < 0.0001$), which contradicted the trim-and-fill test, which indicated no missing studies (SE = 23).

RESULTS

Average fitness effects

Do herbivorous insects tend to compete? It depends on how fitness and evolutionary ancestry are parameterised (Fig. 1). In the composite fitness taxonomic model (all fitness components combined, nested random effects from taxonomic classification, no fixed effects), the mean fitness effect was significantly less than zero (intercept: −0.30, $P = 0.013$). By contrast, in the composite fitness phylogenetic model (with an explicit phylogeny-derived co-variance structure), the interaction between herbivorous insects had a non-significant impact on fitness, although the mean effect was similar in sign and magnitude (intercept: −0.24, $P = 0.29$). Results were more consistent when fitness changes were measured via changes in abundance; interactions between herbivorous insects were significantly negative in both the taxonomic (intercept: −0.58, $P = 0.0022$) and phylogenetic models (intercept: −0.46, $P = 0.016$). For other fitness components (body size, fecundity, and survival), competition was not significant (Fig. 1).

Variation in fitness effects

Estimated effects of model predictors are given in Supporting Information S5. For the most part, effects were qualitatively similar across response variables. Here we mention only the significant and near significant effects. Significant effects for all fitness components are given in Figs 2 and 3.

Composite fitness

First of all, competition was stronger within than between species (taxonomic model; coefficient = 0.16, $P = 0.047$, phylogenetic model; coefficient = 0.20, $P = 0.027$). Population density negatively affected fitness in the taxonomic model (coefficient = −0.13, $P = 0.067$) and phylogenetic model (coefficient = −0.20, $P = 0.026$). Phylogenetic distance between focal and competitor species decreased competition in the taxonomic model (coefficient = 0.00048, $P = 0.025$). Note that the small coefficient of this effect is partly due to the broad range of phylogenetic distances between species; the greatest phylogenetic distances have a Hedge's g effect size of −0.34 on fitness. In the taxonomic model, competition increased when the focal insect was a sucker and the competitor species was an internal feeder (coefficient = 1.05, $P = 0.018$).

Abundance

Spatial separation had a positive effect on fitness (taxonomic model coefficient = 0.66, $P = 0.014$; phylogenetic model coefficient = 0.71, $P = 0.023$), while incomplete temporal separation had a negative effect on fitness in the taxonomic model (coefficient = −0.54, $P = 0.027$). In contrast to the paucity of significant guild effects in the composite fitness models, we found several for abundance (Supporting Information S5). For brevity, we discuss only the phylogenetic model. Competition was significantly reduced when the competitor was a sucker (coefficient = 1.4, $P = 0.025$), or when both insects were internal feeders (coefficient = 2.7, $P = 0.014$). By contrast, competition was significantly increased when the competitor was an internal feeder (coefficient = −2.3, $P = 0.0096$), and when both insects were sap-feeders (phylogenetic model; coefficient = −1.8, $P = 0.014$).

Other fitness components

Summaries of models on the other fitness components (body size, fecundity and survival) are provided in Supplementary Table S5. Here, we note only that although diet breadth did not have a significant effect on abundance or composite fitness, it did have a significant positive effect on fecundity (taxonomic model coefficient = 0.0056, $P = 0.038$; phylogenetic model coefficient = 0.0057, $P = 0.027$).

DISCUSSION

If we ignore the differences between experiments and between the species that were part of those experiments, it appears that herbivorous insects tend to compete. But when we take those differences into account things are more complicated. How one herbivorous insect affects the fitness of another can depend strongly on many factors, including phylogenetic relatedness, population density, spatio-temporal separation, and feeding guild. Some of these effects are predicted nicely by classic competition theory; competition is more intense at higher population densities and when insect herbivores are more closely related and overlap more in time and space. But classic competition theory fails to predict the effects of feeding

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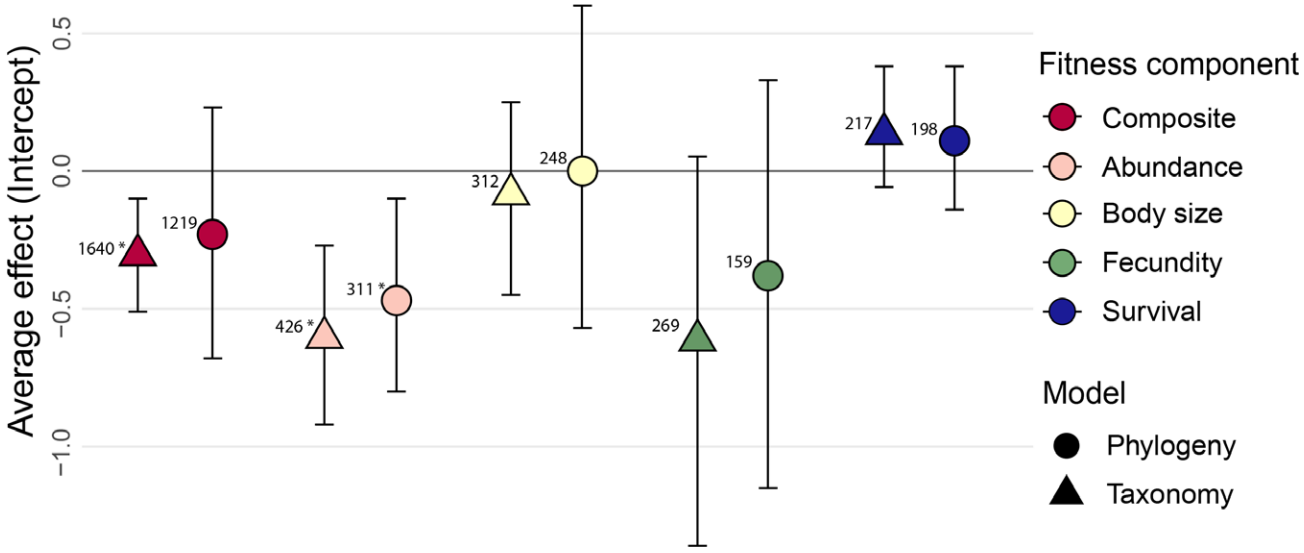

Figure 1 Average effect of interaction between herbivorous insects for each fitness metric. Units are in measurements of Hedges' *g* with units of standard deviation weighted by sample size. Vertical bars give ± 95% high posterior probabilities for effect means, asterisks denote significance to the 0.05 level, the number near each mean effect denotes sample size.

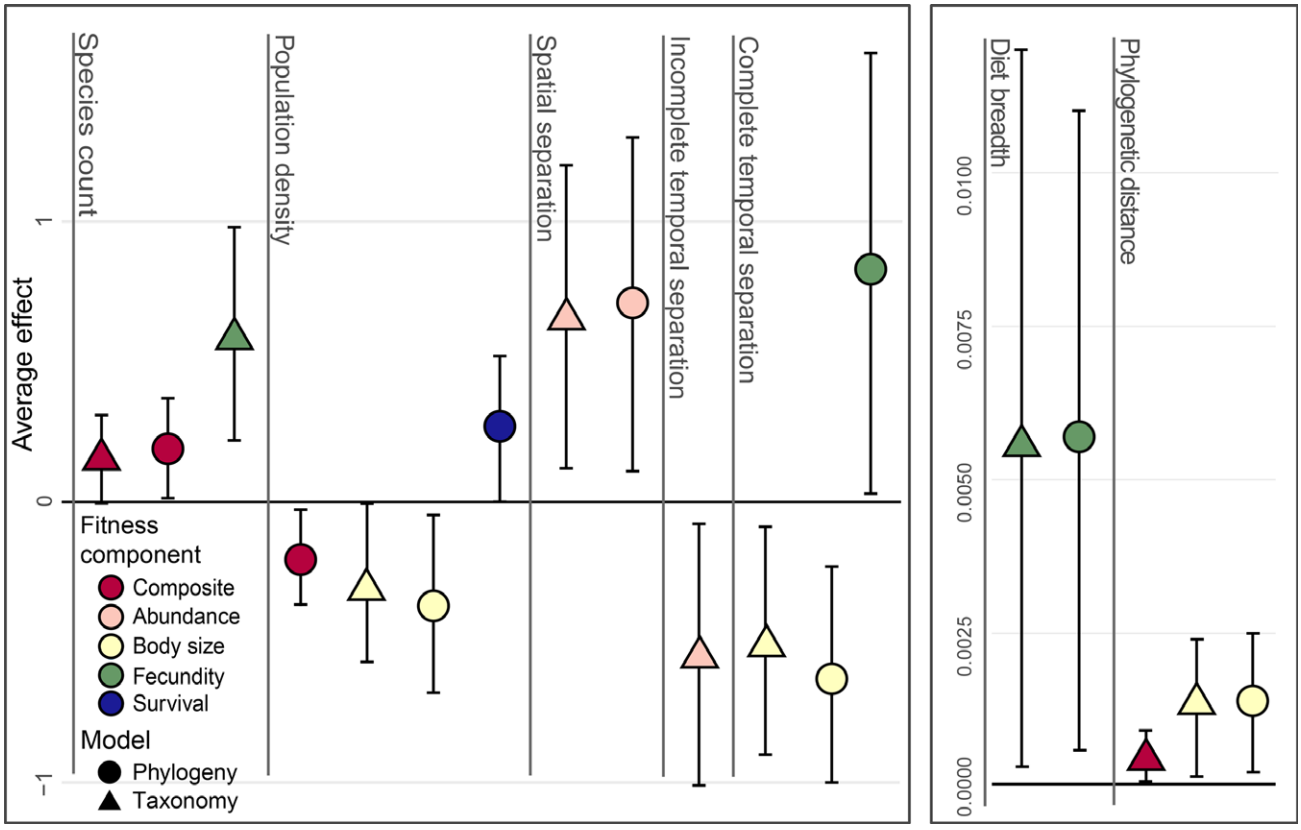

Figure 2 Significant fixed effects for all fitness components. Units are in measurements of Hedges' *g* with units of standard deviation weighted by sample size. Vertical bars give ± 95% high posterior probabilities for effect means. Note that diet breadth and phylogenetic distance are given on a different scale than the other components.

guild; by and large, competition tends to be stronger between insects in different feeding guilds than insects in the same guild. Although this mixture of effects is currently difficult to explain, by estimating them we have made progress. In fact, this is the first study to successfully explain any of the variation in fitness outcomes from herbivorous insect interactions.

Why do our estimates differ from those of previous meta-analyses, in particular Kaplan & Denno (2007)? It could be

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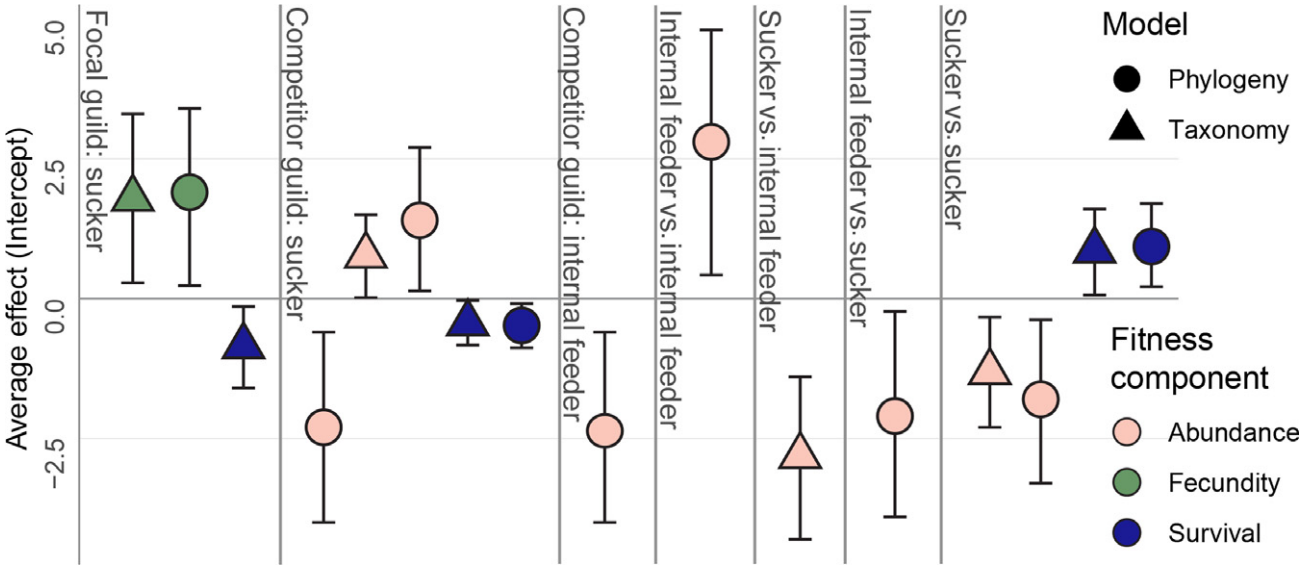

Figure 3 Significant effects from feeding guild on all fitness components. Units are in measurements of Hedges' *g* with units of standard deviation weighted by sample size. Vertical bars give ± 95% high posterior probabilities for effect means. For statistical interaction effects, the focal insect's feeding guild is given first, followed by the competitor insect's guild.

due to differences between statistical models or the data analysed. To find out, we used our statistical models to analyse only the data from Kaplan & Denno (2007). We found some but not all of the same significant effects that we recovered from our main analyses (see Supporting Information S5 for details). Thus, it seems that both the new data and new models have made a difference. Previous meta-analyses have not accounted for phylogenetic non-independence. To get a sense for the influence of phylogeny, we also looked at models of abundance and composite fitness without phylogenetic random effects. For the most part, the results of these models were qualitatively similar to those of the taxonomic model, except that phylogenetic distance and the distinction between within vs between species were not significant effects in the ancestry-free model (see Supporting Information S5). Thus, random phylogenetic effects were influential.

Exactly how we accounted for phylogenetic relatedness also made a difference. These differences could be due to different underlying models of phylogenetic trait evolution, or due to the fact that the phylogenetic models analysed only a subset of the data in the taxonomic models. To rule out the latter, we fit taxonomic models with only the data used by phylogenetic models. We found that the taxonomic model inferences were robust to this sub-setting; the critical difference between models seems to be in the assumptions they make about evolutionary process. To be clear, the only differences we see are in which effects are significant, specifically, the significance of effects from population density, temporal separation, phylogenetic distance, and feeding guild. By contrast, the effects of spatial separation, diet breadth, and the distinction between within and between species interactions were consistent across taxonomic and phylogenetic models. Let us now consider in greater depth some of these effects.

Almost all of the significant negative effects on fitness were between rather than within feeding guilds. But classic competition theory would predict the opposite, as niche overlap should be greater within than between feeding guilds. The interactions between sap-feeders and internal feeders appear to be especially antagonistic. Across models, the fitness of sap-feeders declines when they interact with internal feeders. And in the phylogenetic models of abundance, the fitness of internal feeders decreases in the presence of sap-feeders. Since interactions between internal feeders actually tend to improve fitness, it would seem that direct competition for food is insufficient to explain how internal feeders negatively affect the fitness of sap-feeders (Nyman & Julkunen-Tiitto 2000; Giron *et al.* 2016). But sap-feeders and internal feeders might induce plant defenses that are especially harmful to each other. Researchers have shown that the plant defenses induced by sap-feeders are distinct from those induced by chewers (Ali & Agrawal 2012). Given that internal feeders are known to induce dramatic changes in the physiology of their hosts, the same could also be true of sap-feeders and internal feeders, but more research is needed in this area (Oliveira *et al.* 2016).

The only cases in which within feeding–guild interactions were significantly negative were the effects on abundance and survival when both of the interacting species were sap-feeders. Why would these interactions be especially negative? It could be because sap-feeders tend to reproduce rapidly and form dense and persistent aggregations on their hosts. Internal feeders also have persistent relationships with their hosts, but seldom reproduce as rapidly or form such dense aggregations (Ibbotson & Kennedy 1951; Hardy *et al.* 2018). It could also be because the relatively poor diet of sap-feeders leaves them especially vulnerable to changes in host plant physiology (Hardy 2018).

In accord with classic competition theory, we found that competition tends to be fiercer at higher population density. Nevertheless, we also found that on average herbivorous insects compete even at low densities; in the phylogenetic

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model of composite fitness, the model intercept remained significantly negative even after accounting for the effects of changing density. In other models, population density did not have a significant effect on fitness. Thus, competition could be important at the low densities typical in nature. However, our parameterisation of population density was quite coarse; we were only able to distinguish between experiments in density increased in treatments, from those in which it was held constant. Densities were likely artificially high even in experiments that did match control and treatment densities. In fact, density is only one of several differences between experimental and natural conditions that could affect the outcome of an interaction between herbivorous insects. For example, in the field, in contrast to most experimental designs, insects might disperse away from poor conditions. Such dispersal would have a cost, but one that could be cheaper than the cost of poor performance on a crowded host. Published experiments have also tended to greatly simplify communities. In most studies, only two herbivores interact on one host. And even when designs are more complicated these are nowhere near as complex as what might happen in the field. In particular, more experiments with tri-trophic designs could allow us to address fascinating questions about associational susceptibility and resistance (Wahl & Hay 1995). We look forward to future studies like this.

When assaying fitness effects of herbivorous insect interactions, researchers have tended to look at agricultural pests, which tend to be generalists. Hence the frequency distributions of these species' diet breadth do not match what is typically found in nature (Forister *et al.* 2015). Nevertheless, the estimated effects of diet breadth on competition were robust to the manner in which diet breadth was parameterised (as a continuous trait or as binary factor distinguishing between one-host-family specialists and multiple-host-family generalists). Hence, it seems unlikely that our results have been biased by a data set enriched for generalists.

In most models of abundance and composite fitness, competition is exacerbated by spatial contact. This is consistent with predictions from classic competition theory. The phylogenetic model of abundance also indicated that incomplete temporal separation (where a competitor species has a head start on a common host) tends to increase competition. This could reflect the gradual accumulation of induced plant defenses and natural enemies; an early window of time for feeding before these changes could have lasting impacts on fitness.

The estimated effects of diet breadth on competition were not what would be expected under the traditional view of herbivorous insect diversification, in which speciation is driven by adaptive diet specialisation (Ehrlich and Raven 1964; Futuyma & Moreno 1988). In models of composite fitness and abundance, we found no evidence that competition depends on diet breadth. Up to this point, little evidence has been found of the adaptiveness of diet specificity, whereas considerable evidence supports that diet generalism can be relatively cheap and advantageous (e.g. Agosta & Klemens 2008; Peterson *et al.* 2015, 2016). The adaptiveness of diet specificity might have been in the boost it gave to an herbivore competing for host resources. But instead, we found a weak but significant positive effect of the focal species' diet breadth on fecundity. If anything, it looks as though more polyphagous species are superior competitors. This can be added to the list of challenges for any explanation of herbivorous insect diversification via host use specialisation.

We found evidence of extensive facilitation. Nearly a quarter of our Hedge's g effect sizes were > 0.30, indicating that the interaction substantially increased the fitness of the focal species. One herbivore can increase the fitness of another by helping to overwhelm host defenses, distract natural enemies, or improve habitats, for example, by creating leaf mines and rolls (Bronstein 2009; Karban *et al.* 2012; Soler *et al.* 2012). Although it was not our main focus, we also used our data to try and predict facilitation by estimating the same fixed effects on categorical transformations of our response variables (Supporting Information S5). Specifically, we classified each effect size as either facilitation (Hedge's $g \geq 0.30$), competition (Hedge's $g \leq -0.30$) or no effect ($-0.29 <$ Hedge's $g < 0.29$). We found that facilitation was more likely between than within species (composite phylogeny model, coefficient = 6654.6, $P = 0.022$) and more likely among distantly related species than among closely related species (composite taxonomy model, coefficient = 0.18, $P = 0.047$). This suggests that facilitation is more likely when direct competition.

CONCLUSIONS

What causes competition between herbivorous insects? The last meta-analyses of herbivorous insect interactions (Kaplan & Denno 2007; Radville *et al.* 2014) provided little resolution. Competition was frequent but could not be predicted by indicators of niche overlap, such as phylogenetic relatedness and physical proximity. This was taken to mean that competition among herbivorous insect was largely indirect and mediated via adjacent trophic levels. But note that this interpretation was based largely on a lack of evidence for strong direct interactions. Here, we go further. We identify ways in which the classic theory of direct competition does successfully explain the fitness effects of herbivorous insect interactions: herbivorous insects are more likely to compete when they occur at higher densities, are more closely related, and come into direct contact. Moreover, we find significant statistical evidence *against* certain predictions of the classic theory. Specifically, it seems that in many cases competition tends to be more intense between than within feeding guilds. These latter results underscore the need of accounting for indirect interactions that remain poorly understood. From our perspective, a priority for improving that understanding should be experimental studies on herbivorous insect interactions that are more explicitly tri-trophic along with further study of the molecular mechanisms of induced host plant defense.

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AUTHORSHIP

GB and NH conceived of the project. GB collected the data and conducted the modeling with AW. CK performed phylogenetic analyses. All authors contributed to the writing of the manuscript.

DATA ACCESSIBILITY STATEMENT

No new data were used in this study.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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