REVIEW AND SYNTHESIS

Bottom-up vs. top-down effects on terrestrial insect herbivores: a meta-analysis

Mayra C. Vidal* and
Shannon M. Murphy

*Department of Biological Sciences
University of Denver Denver, CO,
USA*

*Correspondence:
E-mail: mayra.vidal@du.edu*

Abstract
Primary consumers are under strong selection from resource ('bottom-up') and consumer ('top-down') controls, but the relative importance of these selective forces is unknown. We performed a meta-analysis to compare the strength of top-down and bottom-up forces on consumer fitness, considering multiple predictors that can modulate these effects: diet breadth, feeding guild, habitat/environment, type of bottom-up effects, type of top-down effects and how consumer fitness effects are measured. We focused our analyses on the most diverse group of primary consumers, herbivorous insects, and found that in general top-down forces were stronger than bottom-up forces. Notably, chewing, sucking and gall-making herbivores were more affected by top-down than bottom-up forces, top-down forces were stronger than bottom-up in both natural and controlled (cultivated) environments, and parasitoids and predators had equally strong top-down effects on insect herbivores. Future studies should broaden the scope of focal consumers, particularly in understudied terrestrial systems, guilds, taxonomic groups and top-down controls (e.g. pathogens), and test for more complex indirect community interactions. Our results demonstrate the surprising strength of forces exerted by natural enemies on herbivorous insects, and thus the necessity of using a tri-trophic approach when studying insect-plant interactions.

Keywords
Bottom-up, fitness, herbivorous insects, host-plant quality, meta-analysis, natural enemies, parasitoid, predator, top-down.

Ecology Letters (2018) **21**: 138–150

INTRODUCTION

Insect herbivores are one of the most diverse groups of organisms known and are important model organisms for studies of resource specialisation and niche breadth (e.g. Futuyma & Moreno 1988), ecological speciation (e.g. Funk *et al.* 2002; Rundle & Nosil 2005), coevolution (e.g. Ehrlich & Raven 1964), and food web dynamics (e.g. Schmitz 1994). Herbivorous insects are under strong selection from bottom-up forces via their host plants and top-down forces via natural enemies (Ehrlich & Raven 1964; Singer & Stireman 2005). Today it is accepted that both bottom-up and top-down selective forces influence an herbivore's evolution, distribution and population dynamics; however, we still do not know how the relative importance of these selective forces varies across habitats, diet breadth and feeding guilds. The comparative importance of resource ('bottom-up') and consumer ('top-down') controls have been investigated for primary producers in terrestrial (Gruner *et al.* 2008) and marine (Poore *et al.* 2012) ecosystems, but not yet for higher trophic levels. Thus, we performed a meta-analysis to test the relative importance of bottom-up and top-down forces on the fitness of primary consumers, which have significant effects on abundance of primary producers (Gruner *et al.* 2008; Poore *et al.* 2012); we focused our analysis on herbivorous insects due to their enormous diversity compared with other primary consumers and long history of study.

Plant characteristics such as nutritional quality, chemical and mechanical defences, distribution and abundance can have detrimental impacts on insect herbivore fitness and these bottom-up effects have received much attention throughout the history of studies of insect-plant interactions (Schoonhoven *et al.* 2005; Price *et al.* 2011 and references therein). Because plants are not equally suitable as hosts due to variation in chemical or mechanical defences that hamper consumption by herbivores (Fraenkel 1959; Feeny 1970), bottom-up effects were long thought to be more important than top-down effects in regulating herbivore populations. Yet the idea that herbivores may not be limited by resources, but instead by higher trophic levels was proposed early in the literature ('the world is green hypothesis' Hairston *et al.* 1960) and received more attention after Price *et al.* (1980) and Bernays & Graham (1988) re-emphasised the importance of top-down forces on herbivore fitness. However, most hypotheses proposed and tested to investigate diet breadth evolution and herbivore macroevolution are based primarily on bottom-up forces (i.e. host plant use; e.g. Janz & Nylin 2008; Hardy & Otto 2014; Hardy *et al.* 2016; Mason 2016), whereas relatively fewer hypotheses have been proposed and tested that consider top-down forces (but see Jeffries & Lawton 1984; Singer & Stireman 2005; Mooney *et al.* 2012). Two examples of hypotheses that do consider tri-trophic interactions are the enemy-free space hypothesis, which predicts that insect herbivores should feed on host plants associated with lower

susceptibility to natural enemies even if those host plants are otherwise poor quality (Jeffries & Lawton 1984), and the tritrophic interactions hypothesis, which makes predictions about the interactive effects of host-plant quality, natural enemies and diet breadth on herbivore performance (Mooney *et al.* 2012). Studies have also shown that some herbivores face trade-offs between host quality and enemy escape when choosing a host plant (e.g. Thompson 1988; Thompson & Pellmyr 1991; Mira & Bernays 2002; Murphy 2004; Murphy & Loewy 2015).

The purpose of our meta-analysis was to quantitatively analyse the relative impacts of bottom-up and top-down forces on primary consumers, focusing on fitness-related measures for insect herbivores, and to test related paradigms. We evaluated research publications that measured both bottom-up and top-down effects on the same insect herbivore (or community of herbivores) at the same time. We analysed the effect of bottom-up and top-down forces on measures of herbivore fitness, considering multiple moderators that can modulate these effects: (1) herbivore diet breadth (specialist vs. generalist), (2) feeding guild (sucking, chewing, gall-makers, miners), (3) habitat/environment (natural vs. controlled and subdivisions within each), (4) type of bottom-up effects (plant quality vs. habitat quality), (5) type of top-down effects

(predator, parasitoid, pathogen) and (6) how the fitness effects are measured on the herbivore (abundance, development time, growth, mass, reproduction, survival). Each of these moderators has been well studied and alternative predictions exist as to how they may affect herbivore fitness (Table 1). Our meta-analysis will increase our understanding of tri-trophic interactions and how they are structured independently or interactively by bottom-up and top-down selective forces. Previous research supports the positive effects of host plant quality (e.g. Feeny 1970; Coley *et al.* 1985; Agrawal 1998; Eubanks & Denno 2000; Gruner *et al.* 2005) and negative effects of natural enemies (e.g. Holt & Lawton 1994; Marquis & Whelan 1994; Lill *et al.* 2002; Singer & Stireman 2003; Murphy 2004; Long & Finke 2014) on herbivore fitness, yet the relative importance of top-down and bottom-up selective forces on herbivores remains unknown. By conducting a meta-analysis that only included studies that measured *both* bottom-up and top-down effects on a focal herbivore, we were able to quantitatively assess the relative magnitudes of these selective forces for herbivorous insects. Comparing these results with model predictions will improve the development of ecological hypotheses to better understand diet breadth evolution and speciation of herbivores, and their macroevolutionary relationship with host plants and natural enemies.

Table 1 Predictions of the direction of response for each moderator that we analysed.

Moderator	Hypothesis	References	Results follow prediction?	Data used	Figure
Force type	Bottom-up and top-down forces are both important to herbivore fitness.	1–4	Y	All	2b
	Top-down forces have stronger effect on herbivores than bottom-up forces.	8,9 (but see 5–7)	Y		
Diet breadth	Top-down forces are stronger for specialists than generalists.	10 (but see 4,11)	N	Chewers	3a
	Bottom-up forces are stronger for generalists than specialists.	7,12	N		
Feeding guild	External feeders are more affected by top-down forces than internal feeders.	13	N	All	3b
	Sucking insects are less affected by bottom-up forces than other feeding guilds.	14,15	N		
Environment	Bottom-up and top-down forces are stronger in controlled than natural environments.	16,17	N	All	3c and d
	Top-down forces are similar in natural and controlled environments.	13,18	Y		
Bottom-up type	Host plant and habitat quality have similar effects on herbivores.	19	Y	Bottom-up	4a
Top-down type	Parasitoids have stronger effect on herbivores than predators.	13	N	Top-down	5a–c
	A community of natural enemies has a stronger effect on herbivores than a single species.	16,20 (but see 21,22)	N		
	Invertebrate predators have stronger effect on herbivores than vertebrate predators.	23,24 (but see 25)	N	Predator (chewers only)	
Fitness measure	Impact of selective forces are more apparent for direct fitness measures than indirect fitness measures.	26	N	Bottom-up or top-down	4b, 5d

(1) Price *et al.* (1980); (2) Denno *et al.* (2005); (3) Singer & Stireman (2005); (4) Mooney *et al.* (2012); (5)Dethier (1954); (6) Fraenkel (1959); (7) Ehrlich & Raven (1964); (8) Hairston *et al.* (1960); (9) Bernays & Graham (1988); (10) Dyer & Gentry (1999); (11) Dyer (1995); (12) Cornell & Hawkins (2003); (13) Hawkins *et al.* (1997); (14) Raven (1983); (15) Peterson *et al.* (2016); (16) Letourneau *et al.* (2009); (17)Rowen & Kaplan (2016); (18) Halaj & Wise (2001); (19) Price (1991); (20) Griffiths *et al.* (2008); (21) Finke & Denno (2005); (22) Vance-Chalcraft *et al.* (2007); (23) Barber & Marquis (2011); (24) Mooney (2007); (25) Mooney *et al.* (2010); (26) Roitberg *et al.* (2001).

METHODS

Data survey

In our data survey, we included only studies that measured both bottom-up and top-down effects on the same focal herbivore. We compiled publications from two sources: searches of Web of Science using different combinations of key-words of studies done from 2000 to 2015 and publications cited in the review by Walker & Jones (2001). We searched for publications using ISI Web of Science on January 6 and February 2–4, 2016. We used different combinations of the search terms: top-down, bottom-up, insect herbivore, tri-trophic, predator, parasitoid, pathogen, performance, and plant. Our initial survey yielded 1617 publications. We then excluded any publications that did not focus on terrestrial systems (e.g. aquatic systems), did not measure both bottom-up and top-down forces, or were not in English. We also excluded studies of ant-plant mutualisms or competition between herbivores that had no measure of the effect of bottom-up and/or top-down forces on the focal herbivore outside the protective mutualist or competitive interaction; meta-analyses on these topics have already been done (e.g. Kaplan & Denno 2007; Chamberlain & Holland 2009). We also excluded publications that used indirect measures of bottom-up and top-down forces, such as herbivory, richness of herbivores, and/or abundance and richness of natural enemies without measures of attack or direct effects on herbivores. This first review winnowed the pool of 1617 publications down to 178 publications. We then performed a secondary review to determine if each of these 178 studies included both bottom-up and top-down measures for the same herbivore, many of which did not. Any publication that was rejected during this secondary review for not including bottom-up and top-down measures for the same herbivore was independently read by both co-authors before being excluded. Our secondary review yielded 112 publications. However, of these 112 publications, many did not include measures of error on the top-down effect, which is required to weight individual case studies in meta-analyses; we were able to extract standard deviation from 75 of these publications, which were kept in our analysis. Citations for the 112 publications are listed in the Supplementary Information (Table S1).

Effect size measures

To calculate effect sizes for the meta-analysis, we used log response ratio (RR):

$$RR = \ln(\text{mean treatment/mean control})$$

Some researchers prioritise using RR because it is not biased by differences in sample size among experiments and usually follows a normal distribution (Hedges *et al.* 1999; Gruner *et al.* 2008).

For bottom-up effects, we considered the treatment as the effect that is expected to have a positive impact on herbivore fitness. For example, Murphy (2004) reared Alaskan swallowtail (*Papilio machaon aliaska*) larvae on different host plants: the ancestral host (*Cnidium cnidiifolium*), which was high quality, and a novel host that was low-quality (*Petasites frigidus*).

In this example, larvae reared on plants of high quality (the ancestral host) would be the treatment and larvae reared on plants of low quality (the novel host) would be the control. Thus, a significant positive effect size for bottom-up forces means that herbivores had greater fitness on high quality host plants than on poor quality host plants.

For top-down effects, we considered the treatment as the condition (e.g. host plant or habitat) for which herbivores were less negatively-impacted by natural enemies (or where natural enemies were excluded) than in the control. For example, insects reared on plants where enemies were excluded would be the treatment and insects reared in the presence of enemies would be the control. As another example of a comparison in which natural enemies were not excluded, Murphy & Loewy (2015) found that fall webworm (*Hyphantria cunea*) larvae suffered fewer attacks from parasitoids on crabapple (*Malus* spp.), which we classified as our treatment, than on chokecherry (*Prunus virginiana*), which was our control. Thus, a significant positive effect size for top-down forces means that herbivores had greater fitness when natural enemies were absent or exerted lower pressure and therefore that natural enemies had a negative impact on herbivore fitness. When a study included development time of the herbivore or consumption by predators, we switched the treatment and control, since shorter development time or lower consumption by predators is associated with greater herbivore fitness (Price *et al.* 1980). When the top-down effect was measured as percentage parasitism or mortality, we used the percent survival (e.g. if 60% were parasitised, then 40% survived). In our figures, we show the positive effect of plants and negative effect of natural enemies both as positive effect sizes for ease of comparison.

Sometimes the treatment used to calculate the bottom-up effects was the same as the treatment used to calculate the top-down effects, however, that was not the case for every study and it depended on how the experiment was designed. For example, in an experiment that used open and closed cages on different quality plants, we would use the results from only the closed cages (no enemies) to assess the different plant qualities for our bottom-up treatment and control, but we would use the results from the closed and open cages paired by host plant as our top-down treatment and control. Similarly, in an experiment that tested the natural occurrence of natural enemies, the plants with low and high enemy pressure were not necessarily the same plants used for the bottom-up effect size. Experimental design also affected the fitness measures taken on herbivores subjected to different top-down and bottom-up forces. For example, Murphy (2004) used pupal mass, growth rate and survival to pupation as bottom-up fitness measures, but larval survival in the field as the top-down fitness measure; thus, for this example, the fitness measures all differed between bottom-up and top-down treatments and controls. Additionally, there were also more data points for bottom-up than for top-down for this experiment as well as for a few others, which explains why we have greater sample size for bottom-up than top-down forces.

When publications included mean and standard error/deviation in the text, we used this information, whereas when publications included only mean and standard error/deviation on graphs, we assessed those values using PlotDigitizer®. Some

studies included multiple bottom-up treatments (e.g. survival on multiple host plants), and in this case we compared only the two extremes (e.g. survival on the highest and lowest quality host plants) or the highest value compared with the second lowest value if the lowest value was zero. When measures were taken over time, we only included comparisons taken at the last time point (or the one before that if the last measure was zero). Some publications studied more than one herbivore species, and as long as each had independent bottom-up and top-down measures, we analysed them as different entries. Many studies of tri-trophic interactions use percent survival or percent attack by natural enemies as a measure of fitness, however these percentages often do not include standard deviations; of the 112 publications that we found, 37 did not compute standard error/deviation and we could not include them in our analysis.

Impact of bottom-up and top-down measures on herbivores

We tested the overall strength of bottom-up vs. top-down forces and whether the strength of bottom-up or top-down forces varied by diet breadth (specialist, generalist), herbivore feeding guild (sucking, chewing, miner, gall-maker), herbivore taxonomy (order), and habitat/environment type (natural, controlled). Diet breadth is a continuum, but for simplicity we considered specialists as herbivores that feed on fewer than three plant families, while generalists feed on more than three families; we used this threshold because it has historically been used in other studies of insect-plant interactions (Bernays & Graham 1988; Ali & Agrawal 2012). We based classifications of diet breadth from the classification used in the study, or when not reported from our own knowledge or an internet search. The feeding guild (or feeding behaviour) of gall-makers and miners can be considered as chewing herbivores by some authors since they use mandibles to grind the food (Schoonhoven et al. 2005). However, we considered these internal feeders as separate guilds from chewers because their relationship with the plant and natural enemies is expected to differ from chewing herbivores that feed externally (Table 1). Additionally, we considered the possible effect of bottom-up and top-down forces on the herbivore's order, which included Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, and Orthoptera; however, because most orders are confounded with feeding guilds, we only show the results for taxonomic order in the supplementary material. Lastly, we tested whether strength of bottom-up or top-down forces depended on whether the study was conducted in natural or controlled environments as well as subdivisions within each environment type.

Influence of different types of selective forces and types of fitness-related measures

We tested whether the strength of bottom-up forces varied among the different types of bottom-up effects that ecologists study (host plant quality and habitat quality). We used host quality as any measure taken of characteristics intrinsic to the plant, whereas habitat quality measured environmental characteristics that may or may not affect plant quality. Host plant quality included any measure of plant age, architecture, genotype, height, nutritional quality, size, as well as the presence/absence and type of trichomes and/or chemical compounds. Habitat quality included agricultural type, CO_2 variation, elevation, flood regime, fertilisation, salinity, habitat complexity, pollution, spatial variation, temperature variation, and temporal variation; the threshold to define the treatment and control depended on the study system (see Table S2 for more information). We tested whether the strength of top-down forces varied among different types of natural enemy (parasitoid or predator; there were too few studies ($n = 3$) on pathogens to include in the analysis), whether inflicted by a community of enemies or a single species, and whether inflicted by vertebrate or invertebrate predators. We also tested if the response variable used to assess bottom-up and top-down effects on herbivores (e.g. abundance, body mass, developmental time, growth rate, reproduction or survival rate) would elicit different results.

Statistical analysis

For our statistical analysis, we used multi-level error meta-analysis, with publication identity and case identity nested in publication identity as random factors, the moderators and interactions as fixed effects, and RR as the response variable. We used the inverse of variation from each effect size as our weight in the model. We did not consider moderator levels with three or fewer effect sizes because such small sample sizes can cause imprecision in the analysis using random models (Borenstein et al. 2009; Murphy et al. in press). We analysed the type of selective force (top-down or bottom-up) as an individual moderator, and analysed habitat/environment type and subtypes, diet breadth, feeding guild and taxonomic group as the interaction with the selective force type (main effects were also included). We analysed top-down type (natural enemies type, level of organisation, predator type, and fitness measure) only using effect sizes obtained from the top-down data, and similarly analysed bottom-up type only with bottom-up data (Table 1). To test if strength of effect sizes were different, we compared effect sizes between top-down and bottom-up effects, and within bottom-up and top-down effects for each moderator using Tukey's HSD post-hoc test. For our post-hoc test, we used the package *multcomp* and the function *ghlt* to test linear hypotheses, and we used Bonferroni correction when there were more than six comparisons (Hothorn et al. 2008). The estimates and confidence intervals used in the post-hoc comparisons and in our figures were obtained from models including only the interactions compared to a zero intercept, without the main effects. We tested for publication bias using Rosenberg's fail-safe number (Rosenberg 2005) and tested asymmetry (funnel plot Fig. S1) of effect sizes using a *rma.mv* model with the function 'mod=vi' for each dataset. We performed the models using the *metafor* package with *rma.mv* function (Viechtbauer 2010). We performed all statistical tests in R environment 3.4.1 (R Development Core Team 2011). We deposited our data in the Dryad Repository: https://doi.org/10.5061/dryad.2ng06 (Vidal & Murphy 2017).

To control for confounded effects in our data (Fig. 1), we tested the effect of diet breadth only with chewing herbivores because they were the only guild with equal representation of both specialists and generalists. Similarly, we tested the effect

Figure 1 The number of cases for each moderator that we analysed (Table 1 shows each dataset that was used for specific analyses).

of vertebrate and invertebrate predators only with chewing herbivores. We tested the influence of plant and habitat quality on herbivores using the bottom-up natural habitat data, because habitat quality had a good representation in natural habitats (Fig. 1). All of the other moderators were well distributed among subgroups.

We carried out a sensitivity analysis to assess how our initial analysis was sensitive to key features of our dataset. We performed three separate tests to compare with our results:

(1) We removed data from Moon & Stiling (2004), Parry *et al.* (2003) and Santolamazza-Carbone *et al.* (2014), which together had 77 effect sizes of top-down and bottom-up forces (22% of all data) and re-analysed our data to determine if these studies may have significantly affected our results.
(2) We compared the top-down effects from studies using artificial exclusion of natural enemies and studies using natural occurrence of natural enemies.
(3) To test if considering only the extremes in cases with more than one treatment of bottom-up effects may have significantly affected our results, we removed those studies (*n* = 60 effect sizes) and reanalysed our data.

RESULTS

We obtained 356 effect sizes from the 75 publications used in our analysis (Table S1). Fail-safe numbers indicate that the number of unpublished, non-significant studies that would need to be published to negate our significant results is more than 1000 times greater than the number of studies included, and thus our findings are robust against publication bias (fail-safe number = 364,396, $P < 0.0001$). We found asymmetry (i.e. some studies with relatively large sample size also had large residuals, Fig. S1) for the whole dataset ($z = 6.92$,

$n = 356$, $P < 0.0001$), for the bottom-up dataset ($z = 2.88$, $n = 196$, $P = 0.004$), and for the top-down dataset ($z = 2.23$, $n = 160$, $P = 0.02$) (see Fig. 2a for effect size distribution and Fig. S1 for funnel plot). All tests had Q_E with $P < 0.0001$, which shows that there is considerable unexplained heterogeneity among the studies. Most of the studies were conducted since 2000 (Fig. S2), perhaps because of our survey method, and were performed in the United States (Fig. S3a), with the majority from the east coast (Fig. S3b).

Overall impact of top-down and bottom-up forces on herbivores

Top-down forces had a significantly greater effect than bottom-up forces on herbivore fitness ($Q_M = 66.4$, d.f. = 1, $P < 0.0001$, Fig. 2b). The effect size for top-down forces was positive, which means that herbivores had greater fitness in the absence or reduction in natural enemies. For bottom-up forces, the effect size was also positive, which means that herbivores had greater fitness on the highest quality plants or in the best habitats.

Interactions between selective force type and different moderators

Generalist and specialist herbivores were differently affected by top-down and bottom-up forces ($Q_M = 101.48$, d.f. = 3, $P < 0.0001$, Fig. 3a). For specialist chewing herbivores, bottom-up forces were stronger than top-down forces, and bottom-up forces were stronger for specialists than for generalists. Generalists had greater fitness in the absence/reduction in natural enemies, but were not affected by variation in bottom-up forces. Most studies included in our meta-analysis that tested bottom-up effects on specialists used a single host plant species that varied in quality ($n = 28$ of the 33 bottom-up effect sizes), not multiple host plant species; however,
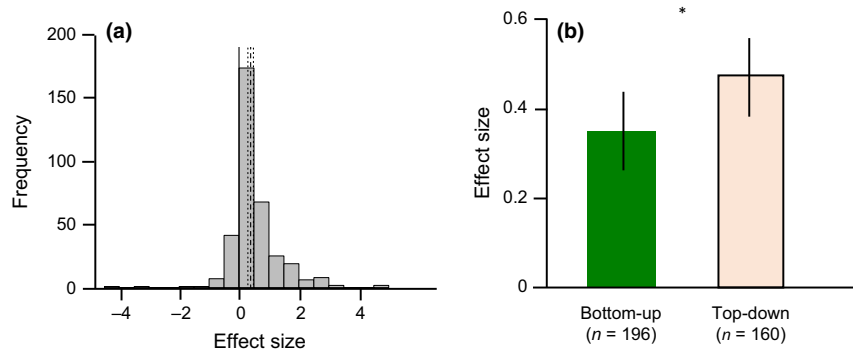
Figure 2 (a) Histogram of effect sizes. Solid line represents zero, dashed lines represents the estimate size with 95% confidence intervals from a null model. (b) Overall bottom-up and top-down effects on insect herbivores. Bars represent the estimate of the model, numbers represent the sample size for each test, and lines represent the 95% confidence interval of the model. If the line crosses zero, it means that the effect size was not significantly different from zero (P from z-test > 0.05). Asterisk represents significant pairwise differences according to post-hoc Tukey's test.
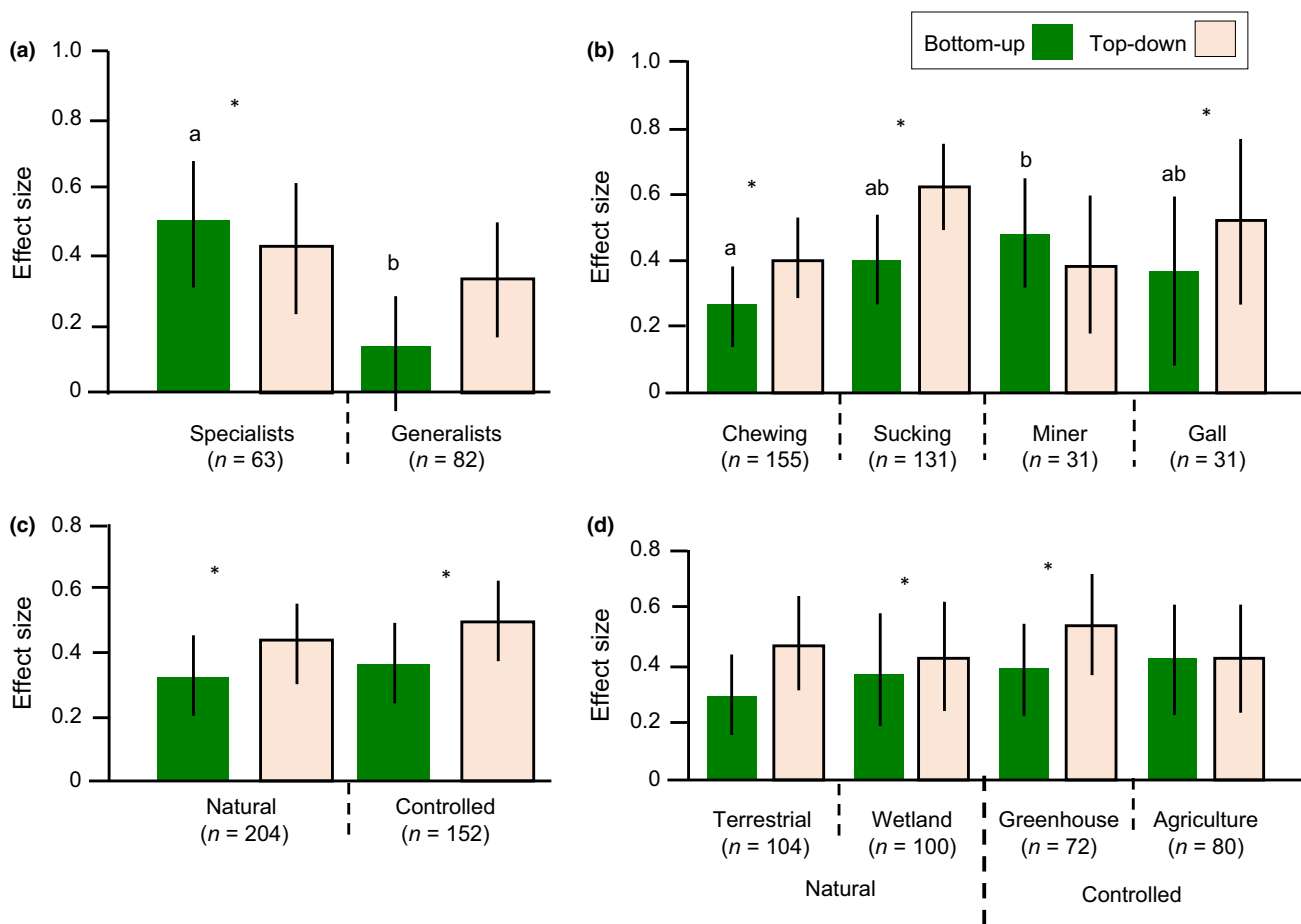

Figure 3 Bottom-up and top-down effects on insect herbivores: (a) that vary in diet breadth (analyses conducted with chewing herbivores only), (b) for each feeding guild, (c) in natural and controlled environments, and (d) in subdivisions of natural and controlled environments. Positive effect sizes for bottom-up and top-down forces show that the herbivore had greater fitness in the treatment (e.g. plant of better quality or in the absence/reduction in natural enemies) than in the control. Bars represent the estimate of the model, numbers represent the sample size for each test, and lines represent the 95% confidence interval of the model. If the line crosses zero, it means that the effect size was not significantly different from zero (P from z-test > 0.05). Asterisks represent significant pairwise differences between bottom-up and top-down forces within each feeding guild or environment type, while letters represent significant pairwise differences within each force type according to *post hoc* Tukey's test.

we found no difference in effect size of bottom-up forces between studies done with either the same vs. different host plants ($Q_M = 0.38$, d.f. = 1, $P = 0.54$).

The feeding guild of the herbivore affected the response of herbivores to selective forces ($Q_M = 122.7$, d.f. = 7, $P < 0.0001$). All feeding guilds were significantly affected by both bottom-up

and top-down forces (Fig. 3b). Notably, top-down effects were stronger than bottom-up effects for chewing, sucking, and gall-making feeding guilds. The strength of top-down forces did not differ significantly among the feeding guilds, whereas bottom-up forces were stronger for miners than for chewing herbivores. Top-down effects were also greater than or equal to bottom-up effects for all taxonomic orders (Figure S4).

Top-down forces were significantly greater than bottom-up forces in both natural and controlled environments ($Q_M = 68.21$, d.f. = 3, $P < 0.0001$, Fig. 3c). The relative effect of top-down and bottom-up forces on herbivores also varied among the different types of controlled and natural environments ($Q_M = 83.66$, d.f. = 7, $P < 0.0001$, Fig. 3d). Top-down forces were significantly stronger than bottom-up for herbivores in wetland and greenhouse environments. We found no significant difference in the strength of top-down or bottom-up forces among the habitat types.

Type of bottom-up forces and fitness measures

The effects of bottom-up forces on herbivore fitness did not differ significantly between studies of habitat and host-plant quality ($Q_M = 1.3$, d.f. = 1, $P = 0.25$, Fig. 4a). We also analysed the type of bottom-up forces with only natural habitat data, in which both habitat and host quality were equally represented, and we found the same pattern ($Q_M = 0.94$, d.f. = 1, $P = 0.33$). We found that the strength of bottom-up forces varied significantly among the types of fitness measure used ($Q_M = 112.86$, d.f. = 5, $P < 0.0001$); the strongest effects were on abundance and survival while the weakest was on development time (Fig. 4b).

Type of top-down forces and fitness measures

Variability in herbivore fitness was not significantly affected by the type of top-down forces ($Q_M = 1.82$, d.f. = 3, $P = 0.61$); predators, parasitoids and both together had equally negative effects on herbivores (Fig. 5a). Similarly, both single species and communities of natural enemies negatively affected herbivores but there were no differences in their

effects on fitness ($Q_M = 0.997$, d.f. = 1, $P = 0.32$, Fig. 5b). Herbivore fitness was not differently affected by the type of predator ($Q_M = 0.69$, d.f. = 1, $P = 0.41$) with both vertebrate and invertebrate predators comparably affecting herbivores (Fig. 5c). Finally, the strength of top-down forces did not vary significantly among the type of fitness measure used ($Q_M = 2.55$, d.f. = 2, $P = 0.28$); however, abundance and survival of herbivores were positively affected by the absence or reduction in natural enemies, but there was no effect on development time (Fig. 5d).

Sensitivity analysis

When we removed the three publications that accounted for 22% of our effect sizes, we found that top-down forces were not significant for miners and growth as a measure of fitness for bottom-up effects was not different from zero. Bottom-up forces were significant for generalist chewing herbivores, but top-down forces were significantly stronger than bottom-up forces. For our second sensitivity analysis, we tested if the type of experimental design of top-down forces could have different effects, and we found that studies using natural occurrence or exclusion of natural enemies were not significantly different ($Q_M = 0.16$, d.f. = 1, $P = 0.69$). Thus, this result shows that whether natural enemies were excluded artificially or varied naturally in the environment (type of top-down experiment) does not affect our findings. For the third sensitivity analysis, we found the same significant effect of bottom-up forces on herbivore fitness even when we removed the studies that only included extreme comparisons of the best and worst quality host plants or habitats ($z = 9.54$, $n = 307$, $P < 0.0001$, estimate = 0.35, lower c.i. = 0.25, upper c.i. = 0.44).

DISCUSSION

Our meta-analysis showed that bottom-up and top-down forces both have consistent impacts on herbivore fitness, but that the effect of top-down forces is significantly stronger than bottom-up forces. Although some historical studies argue that
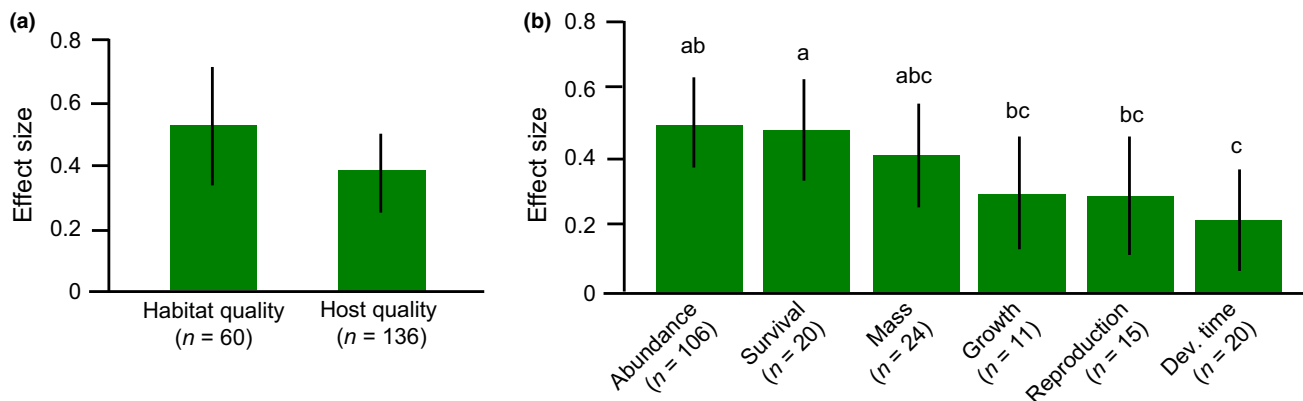

Figure 4 Bottom-up effects on insect herbivores: (a) that vary in host plant quality or habitat quality, and (b) for different measures of herbivore fitness. Bars represent the estimate of the model, numbers represent the sample size for each test, and lines represent the 95% confidence interval of the model. If the line crosses zero, it means that the effect size was not significantly different from zero (P from z-test > 0.05). Letters represent significant differences among fitness measures according to *post-hoc* Tukey's test.
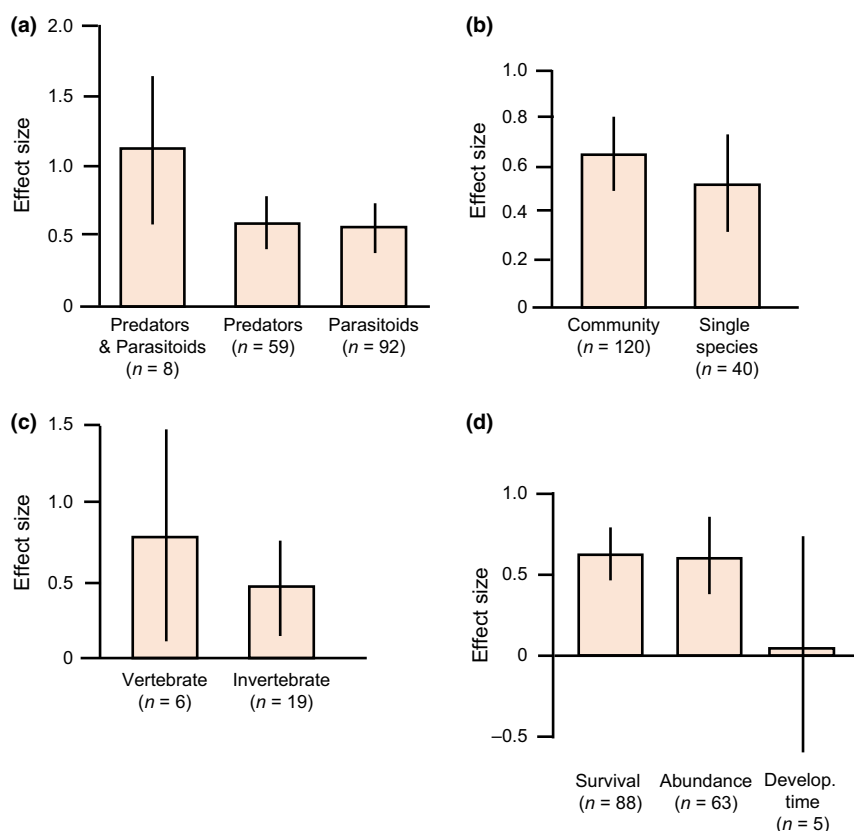
Figure 5 Top-down effects on insect herbivores: (a) for the different kinds of natural enemy, (b) whether a community or single species of enemy was studied, (c) whether the predator was invertebrate or vertebrate, and (d) for different measures of herbivore fitness. Bars represent the estimate of the model, numbers represent the sample size for each test, and lines represent the 95% confidence interval of the model. If the line crosses zero, it means that the effect size was not significantly different from zero (*P* from *z*-test > 0.05).

resources (i.e. plants) are the most important factor regulating populations of primary consumers (e.g. Lindeman 1942; White 1978), our meta-analysis showed that top-down forces are more important for most groups of insect herbivores. Generalist herbivores were only affected by variation in top-down effects, and top-down forces were significantly stronger than bottom-up forces for members of the chewing, sucking, and gall-making feeding guilds. Notably, top-down selective forces were stronger than bottom-up forces in *both* natural and controlled environments.

The influence of diet breadth, feeding guild and habitat on the response of herbivores to top-down and bottom-up forces

Contrary to the overwhelming effect of top-down forces on herbivore fitness for most moderators that we tested, we found a remarkably weak effect of bottom-up forces for generalists. Our results suggest that generalists may be the 'jack of all trades, masters of all' because they did not experience significant bottom-up trade-offs among high and low quality host plants, were less affected by bottom-up forces than specialists, and their fitness did not differ significantly from the fitness of specialists for top-down forces. However, this result is sensitive to sample size as we found a significant effect of bottom-up forces on generalists when we removed the three studies that accounted for 22% of our data; yet, even

excluding these studies, the effects of top-down and bottom-up forces on generalists remained similar to their effects on specialists. There is growing evidence that generalist herbivores do not suffer fitness trade-offs for feeding on different hosts. For instance, our finding that generalists are unaffected by bottom-up forces corresponds with the results of another recent meta-analysis that found that generalists are as likely as specialists to benefit from secondary metabolites of plants (Smilanich *et al.* 2016). Several studies also suggest that generalists are equally fit to feed on the many host plants that they may include in their diet (e.g. Futuyma & Philippi 1987; Agosta & Klemens 2009).

Specialist chewing herbivores were significantly affected by both bottom-up and top-down forces, and it was the only case in which bottom-up forces were stronger than top-down forces. Smilanich *et al.* (2016) found in their meta-analysis that specialists are more negatively affected by plant qualitative defences than generalists, which corresponds with our finding of bottom-up forces being stronger for specialists than generalists. Although the delimitation of diet breadth can be challenging, our results would not have differed had we used a narrower delimitation of diet breadth for specialists given that we found significant bottom-up effects on specialist chewers for studies done with either the same vs. different host plants. However, many specialists will choose to starve rather than feed on an unknown plant, which would have led to an

even greater bottom-up effect if more studies had included non-hosts. Our results demonstrate that even when feeding on their adapted host plants, specialists are still affected by variations in plant or habitat type. However, we conducted the diet breadth analysis using the chewing feeding guild as it was the only guild that had equal representation of both specialists and generalists. Notably, the sucking feeding guild was composed almost entirely of specialists ($n = 123$ of 131 effect sizes) and yet top-down forces were significantly greater than bottom-up forces for this guild. Interestingly, recent work comparing diet breadth evolution of Lepidoptera (which composed most of our chewing guild) and Hemiptera found that caterpillars suffer from more negative trade-offs on fitness when feeding on alternative hosts than true bugs (Hardy *et al.* 2016; Peterson *et al.* 2016). Therefore, to fully analyse the question of how bottom-up and top-down forces differentially affect generalist vs. specialist herbivores, we need more studies on generalist herbivores in guilds other than chewers.

Our results lend additional support to the idea that specialist and generalist herbivores are similarly affected by top-down forces. Although specialist herbivores may have defences against generalist natural enemies (e.g. ants, Dyer 1995), those defences often have weak or no effect on specialist natural enemies (e.g. Thorpe & Barbosa 1986; Dyer & Gentry 1999). In contrast, generalist herbivores are often heavily affected by generalist predators (e.g. birds, Singer *et al.* 2014). Thus, if specialists are more affected by certain natural enemies and generalists by others, the end result may be a similar impact of top-down forces on both types of herbivores, which is what we found. Notably, top-down forces were stronger than bottom-up forces for chewing herbivores, the feeding guild that we used to test the interaction between diet breadth and force type. Chewers feed on the leaf surface, and are usually exposed and vulnerable to natural enemies (Bernays 1997; Sendoya & Oliveira 2017). Research on the ecology of fear demonstrates that even the mere perception of predation risk can detrimentally affect chewing herbivores (e.g. Schmitz *et al.* 1997; Kaplan *et al.* 2014). Miners were the only guild equally affected by bottom-up and top-down forces. Previous research has found that miners are less attacked by predators than external feeders, but can be heavily attacked by parasitoids (Hawkins *et al.* 1997). In our dataset, half of the top-down data for miners included predators, whereas for gall-makers, the other internal feeder guild, predators composed only one third of the top-down forces and that may explain why top-down forces were stronger than bottom-up forces for gall-makers but not for miners.

Top-down forces were stronger than bottom-up forces for both controlled and natural habitats, demonstrating the consistency of our findings across environments. We also found that each force type was surprisingly equal among habitats (i.e. bottom-up forces did not differ significantly among any of the habitat subdivisions, nor did top-down). A recent meta-analysis found that natural enemy diversity has a stronger negative effect on herbivores in cultivated than natural habitats (Letourneau *et al.* 2009), but the studies included in our analysis did not allow us to account for plant and natural enemy diversity so we could not test this directly. However, our results for top-down effects do agree with those of Halaj

& Wise (2001) and Hawkins *et al.* (1997), in which they found similar effects of top-down forces on herbivores in crops and natural habitats. We note that, as is true for any meta-analysis, our results assume that the variation in strength of top-down and bottom-up forces tested in the literature reflects the variation found in nature. It is possible that experimental designs have been biased towards testing a greater proportion of variation for top-down forces than for bottom-up forces, but the design of our meta-analysis in which we used studies that tested the two forces on the same herbivore at the same time mitigates this potential effect.

Influence of different types of selective forces and fitness-related measures on herbivores

Insect herbivores are significantly impacted by bottom-up effects of both host quality and habitat quality, which is notable because our results indicate that both direct measures of plant quality as well as more indirect measures of habitat quality have similar overall effects on herbivores. Interestingly, although both host plant quality and habitat quality are bi-trophic measures, they are both known to affect tri-trophic interactions. Indeed, plant traits can have variable effects on insect herbivores, and even interact with higher trophic levels (e.g. volatiles, Rowen & Kaplan 2016; De Moraes *et al.* 1998). For instance, many studies included in our meta-analysis that investigated how variation in habitat quality affects the strength of selective forces were performed in salt marshes and tested the effect of fertilisation and/or salinity on herbivores. Fertilisation can increase the nutrients available in the plant, and therefore benefit herbivores, but fertilisation can also positively affect higher trophic levels and thus regulation of herbivore populations (Wimp *et al.* 2010). For example, Murphy *et al.* (2012) found a positive effect of fertilisation on herbivores and natural enemy populations, with stronger responses by predators than by herbivores to this bottom-up effect. Bottom-up and top-down cascades are both well studied, and it is clear that both forces can influence each other (e.g. Halaj & Wise 2001).

Predators and parasitoids both negatively affected herbivore fitness. The negative effects of communities or single species of natural enemies, as well as of vertebrate and invertebrate predators, were surprisingly equal. Although predators can have negative effects on parasitoids (intraguild predation, e.g. Snyder & Ives 2001), even for studies that tested parasitoids and predators together we found a similar and negative effect on herbivores compared to studies of either type of natural enemy separately. A community of natural enemies has sometimes been expected to have a more detrimental top-down effect on herbivores than a single enemy species, since a community would likely be composed by different types of natural enemies that can affect the herbivore differently, some being able to avoid herbivore protective mechanisms (Sih *et al.* 1998). However, the effect of a community of natural enemies can be either reduction or enhancement of risk, and so far studies have found support for both cases (Sih *et al.* 1998; Schmitz 2007). For example, Finke & Denno (2005) found that increasing the number of predators decreased prey suppression via intraguild predation. Similarly, vertebrate

predators are often regarded as intra-guild predators that can suppress other natural enemies of the herbivores (Rosenheim 1998). By feeding on other natural enemies, vertebrate predators may end up lessening the pressure exerted by invertebrate natural enemies on herbivores, and thus may even have a positive or null effect on herbivores. However, a recent meta-analysis found an effect of vertebrate insectivores on both herbivores and their arthropod predators, but with a negative resulting effect on herbivores (Mooney et al. 2010).

Our meta-analysis suggests that abundance and survival are good measures of fitness to quantify the effects of bottom-up and top-down selective forces on herbivorous insects. Development time is commonly used as an indirect fitness measure in many studies (e.g. Murphy & Loewy 2015) and it is also the basis of the slow-growth high-mortality hypothesis (Price et al. 1980), which is a fundamental hypothesis in plant-insect interactions. However, we found that for top-down effects, development time in treatments and controls were indistinguishable and bottom-up effects also had the weakest effect on development time. Herbivores feeding on plants of lower quality are usually expected to have longer development time, which would indirectly decrease the chance of survival because of more time exposed to adverse weather and natural enemies (Feeny 1976; Price et al. 1980). Furthermore, natural enemies may indirectly influence the growth rate of herbivores, by decreasing the amount of time that herbivores spend feeding to avoid predation (Heinrich 1979). However, parasitoids and predators may have different effects on herbivores with varying development time; slow growing herbivores may suffer greater mortality from predators, but not from parasitoids (Williams 1999). Our sample size for development time was small and more studies are needed to determine its usefulness as a fitness measure (Murphy et al. in press). Although fitness measures are usually taken under more benign conditions than herbivores usually face in natural conditions (Agrawal et al. 2010), we found that there are significant differences in how much top-down and bottom-up forces can affect commonly used fitness proxies.

Further considerations

Our meta-analysis has important implications for future research on primary consumers and indicates areas of research in need of additional attention. For instance, it would be interesting to test if the same pattern that we found for diet breadth of chewing herbivores would be found for generalist and specialists from other feeding guilds such as sucking herbivores, but there are not yet enough studies with generalist herbivores to test this. The greater proportion of studies on specialists compared with generalists likely reflects the disproportionate diversity, but not importance, of each type of diet breadth found in nature. Additional studies are also needed on more diverse insect orders as studies with Lepidoptera and Hemiptera represented the majority of our data. We showed that the relative strengths of each type of selective force varies for most feeding guilds with top-down forces being stronger than bottom-up for all guilds but miners. These varied dynamics in different orders and guilds can provide an opportunity for experimental research on insect physiology as related to processing of plant-derived food, as well as behavioural ecology of defence by insect herbivores under variable ecological contexts. Comparative studies among orders and guilds will help us understand what regulates insect-plant interactions and how they may evolve. Similarly, future investigations on variation in the strength of top-down and bottom-up selective pressures and the evolution of diet breadth will advance our understanding of key evolutionary questions such as why there are so many more specialist than generalist herbivorous insects.

Future studies should also investigate the differential impact of parasitoids, predators and pathogens as enemies of insect herbivores, and the evolutionary dynamics between different types of natural enemies and their herbivorous prey. However, future studies should be careful in choosing the fitness measure to use and how to report it. A large problem that we encountered when performing this meta-analysis is that one third of the studies we found (33%) failed to include any measure of variance for their top-down effect even when they included variance for their bottom-up effect (e.g. Murphy 2004; Murphy & Loewy 2015). Standard error can easily be included in a study by measuring the survival/parasitism rate per maternal line, plant replicate or sampling period, for example, and it is unclear why so many previous studies have failed to do this for top-down measures when we as researchers are clearly thinking about it for bottom-up measures. It is imperative that researchers studying tri-trophic interactions include standard error in their representation of data for *both* their bottom-up and top-down effects so that future syntheses can include a wider range of studies.

More studies are also needed in different environments and especially in the tropics, as current studies are heavily biased towards temperate regions in North America. For most taxa, the tropics have significantly greater biodiversity than temperate regions and it would be interesting to test whether the strength of bottom-up and top-down selective forces differs among biomes, leading to variation in speciation rates. Our results are limited primarily to temperate regions, and the relative magnitudes of bottom-up and top-down effects may differ in tropical regions that are often more biologically complex. The strength of top-down and bottom-up forces can change with climate and latitude; for instance, both top-down and bottom-up effects on herbivores was shown to increase with temperature towards the tropics (Rodríguez-Castañeda 2013). A recent worldwide experiment demonstrated that caterpillars are more heavily predated in the tropics (Roslin et al. 2017). The strength of selective forces varies not only on latitudinal scales, but also regionally and locally, and other authors have already highlighted the importance of a landscape view of interactions (e.g. Gripenberg & Roslin 2007). More experiments are needed to account for landscape variability in tri-trophic interactions to help us understand geographic variation in diet breadth and local adaptation to host plants.

Although our meta-analysis improves our understanding of insect-plant interactions and the selective forces that affect herbivore fitness, we must be cautious with pitfalls associated with an undeveloped view of bi-trophic interactions. Top-down and bottom-up effects are usually interconnected and

the separation into bi-trophic forces only makes sense for simplicity; whenever possible, a multitrophic perspective should be used for studies that measure herbivore response to host/habitat quality and natural enemies. Other interactions not accounted for in the bi-trophic (or even tri-trophic) approach may also influence the response of herbivores to top-down and bottom-up selective forces that regulate herbivores; examples would include competition with other herbivores (Kaplan & Denno 2007) and mutualistic partners of the plant (e.g. Koricheva *et al.* 2009; Vidal *et al.* 2016) or of the herbivore (e.g. Ferrari *et al.* 2004). Therefore, it is always advisable to use a food-web or a community module approach when possible, even though it is more time consuming and labour-intensive. Encouragingly, a few studies included in our meta-analysis did include more trophic levels than plant-herbivore-enemy, but not enough for a separate analysis. Another factor that we could not test in our meta-analysis is the importance of indirect interactions; top-down and bottom-up forces interact in many different ways to impact herbivores, and the effect of one force often directly or indirectly influences the strength of the other force or how the herbivore responds to that force. For instance, plant quality can influence how herbivores respond to predation risk, in which herbivores feeding upon a less nutritious plant might not be able to afford to stop feeding to hide from predators (Kaplan *et al.* 2014).

With these caveats in mind, we strongly recommend that a tri-trophic approach be used to study herbivore-plant interactions to understand what regulates consumer performance, as the bi-trophic approach that focuses only on consumer and resource is clearly too simplistic and ignores a critical part of most interactions, namely natural enemies (higher trophic levels). Our results demonstrate that both top-down and bottom-up effects must be considered when studying the evolution and population dynamics of insect herbivores. Historically, ecologists have argued about whether bottom-up or top-down effects were more important (e.g. Feeny 1970; Bernays & Graham 1988), but our meta-analysis clearly demonstrates that both are significant selective forces and, for most groups, top-down is more important. Many studies considering the macroevolution of insect-plant interactions involve only bottom-up effects, even though the importance of natural enemies on an herbivore's evolution was advocated more than 10 years ago (Singer & Stireman 2005). Other researchers have similarly highlighted the importance of a tri-trophic perspective (e.g. Price *et al.* 1980; Singer & Stireman 2005; Mooney *et al.* 2012), and here we demonstrate that the importance of top-down effects on insect primary consumers has been undervalued.

ACKNOWLEDGEMENTS

AUTHORSHIP

DATA ACCESSIBILITY STATEMENT

REFERENCES

Agosta, S.J. & Klemens, J.A. (2009). Resource specialization in a phytophagous insect: no evidence for genetically based performance trade-offs across hosts in the field or laboratory. *J. Evol. Biol.*, 22, 907–912.

Agrawal, A.A. (1998). Induced responses to herbivory and increased plant performance. *Science*, 279, 1201–1202.

Agrawal, A.A., Conner, J.K. & Rasmann, S. (2010). Tradeoffs and negative correlations in evolutionary ecology. In *Evolution Since Darwin: The First 150 Years* (eds Bell, M.A., Futuyma, D.J., Eanes, W.F., Levinton, J.S.). Sinauer, Sunderland, MA, pp. 243–68.

Ali, J.G. & Agrawal, A.A. (2012). Specialist versus generalist insect herbivores and plant defense. *Trends Plant Sci.*, 17, 293–302.

Barber, N.A. & Marquis, R.J. (2011). Leaf quality, predators, and stochastic processes in the assembly of a diverse herbivore community. *Ecology*, 92, 699–708.

Bernays, E.A. (1997). Feeding by lepidopteran larvae is dangerous. *Ecol. Entomol.*, 22, 121–123.

Bernays, E. & Graham, M. (1988). On the evolution of host specificity in phytophagous arthropods. *Ecology*, 69, 886–892.

Borenstein, M., Hedges, L.V., Higgins, J. & Rothstein, H.R. (2009). When does it make sense to perform a meta-analysis? In *Introduction to Meta-Analysis* (eds Borenstein, M., Hedges, L.V., Higgins, J., Rothstein, H.R.). Wiley, West Sussex, UK, pp. 357–364.

Chamberlain, S.A. & Holland, J.N. (2009). Quantitative synthesis of context dependency in ant – plant protection mutualisms. *Ecology*, 90, 2384–2392.

Coley, P.D., Bryant, J.P. & Chapin, F.S. (1985). Resource availability and plant antiherbivore defense. *Science*, 230, 895–899.

Cornell, H.V. & Hawkins, B.A. (2003). Herbivore responses to plant secondary compounds: a test of phytochemical coevolution theory. *Am. Nat.*, 161, 507–522.

De Moraes, C.M., Lewis, W.J., Pare, P.W., Alborn, H.T. & Tumlinson, J.H. (1998). Herbivore-infested plants selectively attract parasitoids. *Nature*, 393, 570–573.

Denno, R.F., Lewis, D. & Gratton, C. (2005). Spatial variation in the relative strength of top-down and forces: causes phytophagous insect populations and consequences for. *Ann. Zool. Fennici*, 42, 295–311.

Dethier, V.G. (1954). Evolution of feeding preferences in phytophagous insects. *Evolution*, 8, 33–54

Dyer, L.A. (1995). Tasty generalists and nasty specialists? Antipredator mechanisms in tropical lepidopteran larvae. *Ecology*, 76, 1483–1496.

Dyer, L.A. & Gentry, G. (1999). Predicting natural-enemy responses to herbivores in natural and managed systems. *Ecol. Appl.*, 9, 402–408.

Ehrlich, P.R. & Raven, P.H. (1964). Butterflies and plants: a study in coevolution. *Evolution*, 18, 586–608.

Eubanks, M.D. & Denno, R.F. (2000). Host plants mediate omnivore-herbivore interactions and influence prey suppression. *Ecology*, 81, 936–947.

Feeny, P. (1970). Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology*, 51, 565–581.

Feeny, P. (1976). Plant apparency and chemical defense. In *Biochemical Interaction Between Plants and Insects* (eds Wallace, J.W., Mansell, R.L.). Springer, US, pp. 1–40.

Ferrari, J., Darby, A.C., Daniell, T.J., Godfray, H.C.J. & Douglas, A.E. (2004). Linking the bacterial community in pea aphids with host-plant use and natural enemy resistance. *Ecol. Entomol.*, 29, 60–65.

Finke, D.L. & Denno, R.F. (2005). Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecol. Lett.*, 8, 1299–1306.

Fraenkel, G.S. (1959). The raison d'etre of secondary plant substances. *Science*, 129, 1466–1470.

Funk, D.J., Filchak, K.E. & Feder, J.L. (2002). Herbivorous insects: model systems for the comparative study of speciation ecology. *Genetica*, 116, 251–267.

Futuyma, D.J. & Moreno, G. (1988). The evolution of ecological specialization. *Annu. Rev. Ecol. Syst.*, 19, 207–233.

Futuyma, D.J. & Philippi, T.E. (1987). Genetic variation and covariation in responses to host plants by *Alsophila pometaria* (Lepidoptera: Geometridae). *Evolution*, 41, 269–279.

Griffiths, G.J., Wilby, A., Crawley, M.J. & Thomas, M.B. (2008). Density-dependent effects of predator species-richness in diversity-function studies. *Ecology*, 89, 2986–2993.

Gripenberg, S. & Roslin, T. (2007). Up or down in space? Uniting the bottom-up versus top-down paradigm and spatial ecology. *Oikos*, 116, 181–188.

Gruner, D.S., Taylor, A.D. & Forkner, R.E. (2005). The effects of foliar pubescence and nutrient enrichment on arthropod communities of *Metrosideros polymorpha* (Myrtaceae). *Ecol. Entomol.*, 30, 428–433.

Gruner, D.S., Smith, J.E., Seabloom, E.W., Sandin, S.A., Ngai, J.T., Hillebrand, H. *et al.* (2008). A cross-system synthesis of consumer and nutrient resource control on producer biomass. *Ecol. Lett.*, 11, 740–755.

Hairston, N.G., Smith, F.E. & Slobodkin, L.B. (1960). Community structure, population control, and competition. *Am. Nat.*, 94, 421–425.

Halaj, J. & Wise, D.H. (2001). Terrestrial trophic cascades: how much do they trickle? *Am. Nat.*, 157, 262–281.

Hardy, N.B. & Otto, S.P. (2014). Specialization and generalization in the diversification of phytophagous insects: tests of the musical chairs and oscillation hypotheses. *Proc. Royal Soc. B*, 281, 1–10.

Hardy, N.B., Peterson, D.A. & Normark, B.B. (2016). Nonadaptive radiation: pervasive diet specialization by drift in scale insects? *Evolution*, 70, 2421–2428.

Hawkins, B.A., Cornell, H.V. & Hochberg, M.E. (1997). Predators, parasitoids, and pathogens as mortality agents in phytophagous insect populations. *Ecology*, 78, 2145–2152.

Hedges, L.V., Gurevitch, J. & Curtis, P.S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology*, 80, 1150–1156.

Heinrich, B. (1979). Foraging strategies of caterpillars: leaf damage and possible predator avoidance strategies. *Oecologia*, 42, 325–337.

Holt, R.D. & Lawton, J.H. (1994). The ecological consequences of shared natural enemies. *Ann. Rev. Ecol. Syst.*, 25, 495–520.

Hothorn, T., Bretz, F. & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biom. J.*, 50, 346–363.

Janz, N. & Nylin, S. (2008). The oscillation hypothesis of host-plant range and speciation. In: *The Evolutionary Biology of Herbivorous Insects: Specialization, Speciation and Radiation* (ed. Tilmon, K.). University of California Press, Oakland, CA. pp. 203–215.

Jeffries, M.J. & Lawton, J.H. (1984). Enemy free space and the structure of ecological communities. *Biol. J. Linnean Soc.*, 23, 269–286.

Kaplan, I. & Denno, R.F. (2007). Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. *Ecol. Lett.*, 10, 977–994.

Kaplan, I., McArt, S.H. & Thaler, J.S. (2014). Plant defenses and predation risk differentially shape patterns of consumption, growth, and digestive efficiency in a guild of leaf-chewing insects. *PLoS ONE*, 9 (4), e93714.

Koricheva, J., Gange, A.C. & Jones, T. (2009). Effects of mycorrhizal fungi on insect herbivores: a meta-analysis. *Ecology*, 90, 2088–2097.

Letourneau, D.K., Jedlicka, J.A., Bothwell, S.G. & Moreno, C.R. (2009). Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Ann. Rev. Ecol. Evol. Syst.*, 40, 573–592.

Lill, J.T., Marquis, R.J. & Ricklefs, R.E. (2002). Host plants influence parasitism of forest caterpillars. *Nature*, 417, 170–173.

Lindeman, R.L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, 23, 399–417.

Long, E.Y. & Finke, D.L. (2014). Contribution of predator identity to the suppression of herbivores by a diverse predator assemblage. *Environ. Entomol.*, 43, 569–576.

Marquis, R.J. & Whelan, C.J. (1994). Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology*, 75, 2007–2014.

Mason, P.A. (2016). On the role of host phenotypic plasticity in host shifting by parasites. *Ecol. Lett.*, 19, 121–132.

Mira, A. & Bernays, E.A. (2002). Trade-offs in host use by *Manduca sexta*: plant characters vs natural enemies. *Oikos*, 97, 387–397.

Moon, D.C. & Stiling, P. (2004). The influence of a salinity and nutrient gradient on coastal vs. upland tritrophic complexes. *Ecology*, 85, 2709–2716.

Mooney, K.A. (2007). Tritrophic effects of birds and ants on a canopy food web, tree growth, and phytochemistry. *Ecology*, 88, 2005–2014.

Mooney, K.A., Gruner, D.S., Barber, N.A., Van Bael, S.A., Philpott, S.M. & Greenberg, R. (2010). Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. *Proc. Natl Acad. Sci. USA*, 107, 7335–7340.

Mooney, K.A., Pratt, R.T. & Singer, M.S. (2012). The tri-trophic interactions hypothesis: Interactive effects of host plant quality, diet breadth and natural enemies on herbivores. *PLoS ONE*, 7(4).

Murphy, S.M. (2004). Enemy-free space maintains swallowtail butterfly host shift. *Proc. Natl Acad. Sci. USA*, 101, 18048–18052.

Murphy, S.M. & Loewy, K.J. (2015). Trade-offs in host choice of an herbivorous insect based on parasitism and larval performance. *Oecologia*, 179, 741–751.

Murphy, S.M., Wimp, G.M., Lewis, D. & Denno, R.F. (2012). Nutrient presses and pulses differentially impact plants, herbivores, detritivores and their natural enemies. *PLoS ONE*, 7, 1–10.

Murphy, S. M., Vidal, M. C., Hallagan, C. J., Barnes, E. E. & Broder, E. D. In Press. A slow-growth high-mortality meta-analysis for insects: a comment on Chen & Chen. *Insect Sci.*, 10.1111/1744-7917.12459

Parry, D., Herms, D.A. & Mattson, W.J. (2003). Responses of an insect folivore and its parasitoids to multiyear experimental defoliation of aspen. *Ecology*, 84, 1768–1783.

Peterson, D.A., Hardy, N.B. & Normark, B.B. (2016). Micro- and macroevolutionary trade-offs in plant-feeding insects. *Am. Nat.*, 188, 640–650.

Poore, A.G.B., Campbell, A.H., Coleman, R.A., Edgar, G.J., Jormalainen, V., Reynolds, P.L. *et al.* (2012). Global patterns in the impact of marine herbivores on benthic primary producers. *Ecol. Lett.*, 15, 912–922.

Price, P.W. (1991). The plant vigor hypothesis and herbivore attack. *Oikos*, 62, 244–251.

Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N. & Weis, A.E. (1980). Interaction between three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Ann. Rev. Ecol. Syst.*, 11, 41–65.

Price, P.W., Denno, R.F., Eubanks, M.D., Finke, D.L. & Kaplan, I. (2011). *Insect Ecology: behavior*. Cambridge University Press, Populations and Communities.

R Development Core Team, R. (2011). R: A language and environment for statistical computing R. D. C. Team, ed. R Foundation for Statistical Computing, 1(2.11.1), p.409. Available at: http://www.r-project.org. Last accessed 18 October 2017

Raven, J.A. (1983). Phytophages of xylem and phloem: a comparison of animal and plant sap-feeders. *Adv. Ecol. Res.*, 13, 135–234.

Rodríguez-Castañeda, G. (2013). The world and its shades of green: a meta-analysis on trophic cascades across temperature and precipitation gradients. *Global Ecol. Biogeogr.*, 22, 118–130.

Roitberg, B.D., Boivin, G. & Vet, L.E.M. (2001). Fitness, parasitoids, and biological control: an opinion. *Can. Entomol.*, 133, 429–438.

Rosenberg, M.S. (2005). The file-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. *Evolution*, 59, 464–468.

Rosenheim, J.A. (1998). Higher-order predators and the regulation of insect herbivore populations. *Ann. Rev. Entomol.*, 43, 421–447.

Roslin, T., Hardwick, B., Novotny, V., Petry, W.K., Andrew, N.R., Asmus, A. *et al.* (2017). Higher predation risk for insect prey at low latitudes and elevations. *Science*, 356, 742–744.

Rowen, E. & Kaplan, I. (2016). Eco-evolutionary factors drive induced plant volatiles: a meta-analysis. *New Phytol.*, 210, 284–294.

Rundle, H.D. & Nosil, P. (2005). Ecological speciation. *Ecol. Lett.*, 8, 336–352.

Santolamazza-Carbone, S., Velasco, P., Soengas, P. & Cartea, M.E. (2014). Bottom-up and top-down herbivore regulation mediated by glucosinolates in *Brassica oleracea var*. *acephala*. *Oecologia*, 174, 893–907.

Schmitz, O.J. (1994). Resource edibility and trophic exploitation in an old-field food web. *Proc. Natl Acad. Sci. USA*, 91, 5364–5367.

Schmitz, O.J. (2007). Predator diversity and trophic interactions. *Ecology*, 88, 2415–2426.

Schmitz, O.J., Beckerman, A.P. & O'Brien, K.M. (1997). Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology*, 78, 1388–1399.

Schoonhoven, L.M., vanLoon, J.J.. & Dicke, M. (2005). *Insect-Plant Biology* 2nd edition, Oxford Press, Canada.

Sendoya, S.F. & Oliveira, P.S. (2017). Behavioural ecology of defense in a risky environment: caterpillars versus ants in a Neotropical savanna. *Ecol. Entomol.* 42, 553–564.

Sih, A., Englund, G. & Wooster, D. (1998). Emergent impacts of multiple predators on prey. *Trends Ecol. Evol.*, 13, 350–355.

Singer, M.S. & Stireman, J.O. (2003). Does anti-parasitoid defense explain host-plant selection by a polyphagous caterpillar? *Oikos*, 100, 554–562.

Singer, M.S. & Stireman, J.O. (2005). The tri-trophic niche concept and adaptive radiation of phytophagous insects. *Ecol. Lett.*, 8, 1247–1255.

Singer, M.S., Lichter-Marck, I.H., Farkas, T.E., Aaron, E., Whitney, K.D. & Mooney, K.A. (2014). Herbivore diet breadth mediates the cascading effects of carnivores in food webs. *Proc. Natl Acad. Sci. USA*, 111, 9521–9526.

Smilanich, A.M., Fincher, R.M. & Dyer, L.A. (2016). Does plant apparency matter? Thirty years of data provide limited support but reveal clear patterns of the effects of plant chemistry on herbivores. *New Phytol.*, 210, 1044–1057.

Snyder, W.E. & Ives, A.R. (2001). Generalist predator disrupt biological control by a specialist parasitoid. *Ecology*, 82, 705–716.

Thompson, J.N. (1988). Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomol. Exp. Appl.*, 47, 3–14.

Thompson, J.N. & Pellmyr, O. (1991). Evolution of oviposition behavior and host plant preference in Lepidoptera. *Ann. Rev. Entomol.*, 36, 65–89.

Thorpe, K.W. & Barbosa, P. (1986). Effects of consumption of high and low nicotine tobacco by *Manduca sexta* (Lepidoptera: Sphingidae) on survival of gregarious endoparasitoid *Cotesia congregata* (Hymenoptera: Braconidae). *J. Chem. Ecol.*, 12, 1329–1337.

Vance-Chalcraft, H.D., Rosenheim, J.A., Vonesh, J.R., Osenberg, C.W. & Sih, A. (2007). The influence of intraguild predation on prey suppression and prey release: a meta-analysis. *Ecology*, 88, 2689–2696.

Vidal, M.C. & Murphy, S.M. (2017). Data from: bottom-up versus top-down effects on terrestrial insect herbivores: a meta-analysis. *Dryad Digital Repository* https://doi.org/10.5061/dryad.2ng06.

Vidal, M.C., Sendoya, S.F. & Oliveira, P.S. (2016). Mutualism exploitation: predatory drosophilid larvae sugar-trap ants and jeopardize facultative ant-plant mutualism. *Ecology*, 97, 1650–1657.

Viechtbauer, W. (2010). Conducting meta-analysis in R with the metafor package. *J. Stat. Softw.*, 36, 1–48.

Walker, M. & Jones, T.H. (2001). Relative roles of top-down and bottom-up forces in terrestrial tritrophic plant - insect herbivore - natural enemy system. *Oikos*, 93, 177–187.

White, T.C.R. (1978). The importance of a relative shortage of food in animal ecology. *Oecologia*, 33, 71–86.

Williams, I.S. (1999). Slow-growth, high-mortality - a general hypothesis, or is it? *Ecol. Entomol.*, 24, 490–495.

Wimp, G.M., Murphy, S.M., Finke, D.L., Huberty, A.F. & Denno, R.F. (2010). Increased primary production shifts the structure and composition of a terrestrial arthropod community. *Ecology*, 91, 3303–3311.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.