Quantitative measure of fitness in tri-trophic interactions and its influence on diet breadth of insect herbivores

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Abstract. Herbivore-plant interactions should be studied using a tri-trophic approach, but we lack a quantitative measure of the combined effect of top-down and bottom-up forces on herbivore fitness. We propose the combination of the bi-trophic fitness slopes as a tri-trophic fitness measure. We use the relationship between fitness associated with top-down and bottom-up forces and the frequency of host plant use to calculate the top-down and bottom-up fitness slopes, which we then combine to obtain three possible directions of tri-trophic slopes. A positive tri-trophic slope indicates that herbivores have overall greater tri-trophic fitness on the more frequently used hosts. A null tri-trophic fitness slope indicates that herbivores have similar fitness on all host plants. A negative tri-trophic slope indicates that herbivores have generally lower fitness on the more frequently used hosts. We tested the explanation power of our method using data from the literature that tested herbivore host shifts and experimentally using a generalist herbivore with variable diet breadth across populations. We found that in host shifts, herbivores have higher tri-trophic fitness on the novel host, while in generalist populations, herbivores use most frequently the best host available. We present applications in other research areas and consider the limitations of our approach. Our approach is a first step towards a comprehensive model of multiple selective forces acting on the evolution of interactions.

Key words: bottom-up; host shift; niche breadth; selective forces; top-down; tri-trophic interactions.

INTRODUCTION

Resource specialization is ubiquitous in many systems and is directly associated with a variety of ecological and evolutionary processes, such as ecological speciation (e.g., Rundle and Nosil 2005), coevolution (e.g., Ehrlich and Raven 1964), and food web dynamics (e.g., Schmitz 1994). Evolutionarily, resource use is a crucial factor influencing diversification. For instance, expansion onto new resources or environments is one of the key features of adaptive radiation (Schluter 2000, e.g., Winkler et al. 2009) and selective pressure due to competition for resources is one way for natural selection to act (Darwin 1859). Insect herbivores are ideal model organisms to study resource specialization (e.g., Futuyma and Moreno 1988) because the vast majority of herbivorous insects are specialists. Although the study of herbivore diet breadth has spanned many years and yielded exciting insights, we still do not fully understand why there are so many specialist species and so few generalists, as more than 90% of well-characterized insect herbivores feed on fewer than four plant families (Forister et al. 2015).

Most hypotheses proposed to explain diet specialization focus on the possible advantages of being specialists rather than generalists from the perspective of host plant use (Bernays 1998, 2001, Futuyma and Moreno 1988, Jaenike 1990, but see Hardy et al. 2016). For instance, it has long been assumed that herbivores specialize on a specific host species because it facilitates best coping with the defenses of that host plant (Ehrlich and Raven 1964). As a result, specialists are expected to have reduced fitness when feeding on a non-host (as compared to the host plant to which they are adapted). Generalists, on the other hand, would have similar performance on their different hosts, but would overall have lower fitness than specialists (but see Fry 1996). However, evidence from a recent meta-analysis and experiments (Agosta and Klemens 2009, Vidal and Murphy 2018a) suggests that generalists may be the "jack of all trades, master of all" because specialists are more negatively affected by variation in bottom-up forces than generalists, even when feeding on their adapted host plant, and generalists seem able to feed relatively well on their many potential hosts.

Studies meant to understand macroevolutionary patterns of herbivore diet breadth usually do not consider the simultaneous effect of both natural enemies and host plant on herbivore fitness (e.g., Janz and Nylin 2008, Hardy et al. 2016. But see Singer and Stireman 2005, Mooney et al. 2012). The effects of plants (i.e., resource, bottom-up effects) and natural enemies (i.e. top-down effects) have important implications for the evolution and diet breadth of insect herbivores (Singer and Stireman 2005, Mooney et al. 2012, Vidal and Murphy 2018a), and a tri-trophic approach is necessary to understand diet breadth patterns. Here, we introduce a new approach to quantify the effect of tri-trophic interactions on herbivore fitness and we apply our framework to interpret (1) host shifts in different systems and (2) how diet breadth varies in natural populations of a generalist herbivore. Our quantitative measure of fitness assessed through the lens of tri-trophic interactions has the potential to be used in other systems and we discuss how our approach could advance our understanding of resource specialization and diet breadth evolution as well as other questions related to selective pressures.

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Measure of bi- and tri-trophic fitness slopes

Although top-down and bottom-up forces are interconnected in nature, most researchers measure the two forces separately, and we currently lack a way to quantitatively compare them. We propose a simple and straightforward method for measuring tri-trophic fitness by summing the two bi-trophic fitness slopes to estimate the tri-trophic slope (adapted from Singer and Stireman 2005). The addition of the slopes results in a measure similar to the mean of the fitness associated with each bi-trophic force; we test our approach by comparing our results with the mean of the bi-trophic slopes obtained by both resampling and by using Bayesian linear regression (see test II below).

To use our proposed tri-trophic fitness approach, herbivores need to use at least two host plants or have a variable measure of bottom-up or top-down effect (e.g., same host species but of different quality or same host species but with spatial variability in enemy exposure). For each host plant, we first calculate the bi-trophic bottom-up effect (bi-trophic because here we consider only the herbivore and its host plant) on herbivore fitness for both host plants. Then we calculate the bi-trophic top-down effect (bi-trophic because here we consider only the herbivore and its natural enemies) on herbivore fitness. Finally, to calculate the tri-trophic fitness slope, we add the two bi-trophic slopes (or we add the change in bi-trophic fitness, see example in Fig. 1a). Fitness from tri-trophic interactions could alternatively be calculated by multiplying the bottom-up fitness component by the top-down fitness component, which results in a similar direction of tri-trophic slope (i.e. positive, null, or negative). We consider all possible combinations of bi-trophic slopes, which results in three possible tri-trophic fitness scenarios (our examples here consider frequency of host plant use for ease of comparison with our data, but the same conclusions can be made for different comparisons of host use):

I) *Positive tri-trophic slope:* the population (or metapopulation) feeds most frequently on the host on which they have higher tri-trophic fitness compared to the overall fitness associated with less frequently used hosts. When a positive bi-trophic slope is steeper than the negative bi-trophic slope (i.e., greater difference in top-down or bottom-up fitness across frequency of host use) or when both bi-trophic slopes are positive, it results in a positive tri-trophic slope (Fig. 1b, top row). In comparisons of multiple hosts, the fitness associated with the selective forces may be high for some plants that are used in low frequency, but when considering all plants, the trend would be to have higher fitness associated with the tri-trophic interaction on more frequently used plants.

II) *Null tri-trophic slope:* the population (or metapopulation) feeds on different hosts that have equal tri-trophic fitness. When the negative and the positive bi-trophic slopes have equal value or cancel each other, the resulting tri-trophic slope would be null (Fig. 1b, middle row). Again, the variation in fitness found when studying herbivore performance on multiple host plants may show the herbivore to have higher fitness on some hosts compared to others, but our slopes consider the overall trend across all hosts and not individual comparisons between hosts.

III) *Negative tri-trophic slope:* the population (or metapopulation) tends to feed most frequently on the hosts on which they have lower tri-trophic fitness. If the negative bi-trophic slope is steeper than the positive bi-trophic slope (i.e., lower top-down or bottom-up fitness on the most frequently used host) or both bi-trophic slopes are negative, the resulting tri-trophic slope would be negative (Fig. 1b, bottom row).

We add the bi-trophic slopes to calculate the tri-trophic slope because both bi-trophic slopes are calculated using the same variables: fitness as dependent variable and host plant use as independent variable. To make this addition possible, these two variables should be comparable between the two bi-trophic slopes (i.e., one measure cannot exceed 2x the top range of the other measure). In our examples, we mostly use survival for both bi-trophic slopes and a measure of mass, which are fitness proxies well supported in studies with insect herbivores (Honěk 1993, Crone 2001). Notably, the performance measures associated with the top-down and bottom-up forces should be of similar scale (we discuss this and other potential problems in the 'Limitations' section below) and need to be reliable and tested fitness proxies. Therefore, for our tests both bottom-up and top-down slopes consider survival and are in the same scale.

Methods

Test I – Proof of concept using host shifts by multiple insect herbivore taxa

A consistent approach should be applicable to different taxa and independent of sampling methods. To test the consistency of our tri-trophic fitness approach, we applied it to tests of herbivore host shifts from the published literature; we used studies that measured both top-down and bottom-up forces on the herbivore. Herbivores can experience increased fitness on a novel host compared to an ancestral host through reduced attack from natural enemies (e.g., Murphy 2004) despite novel hosts apparently being of reduced plant quality (Yoon and Read 2016). Considering the enemy-free space hypothesis, we would expect that the advantage of escaping enemies should trump the disadvantage of feeding on a poor quality plant (Berdegue et al. 1996). Thus, the top-down slope should be positive and have a greater absolute value than the bottom-up slope, which should be negative (the herbivore experiences a trade-off between poor host plant quality and survival from natural enemies on the novel host). Therefore, the herbivore's tri-trophic fitness should be greater on the novel host than on the ancestral host, and hence the resulting tri-trophic slope would be positive (Fig. 1b top row). Alternatively, the herbivore can have similar tri-trophic fitness on the ancestral and novel hosts, which would not select against using the ancestral host plant with expansion to include the novel host (e.g., host range expansion), and hence the resulting tri-trophic slope would be null (Fig. 1b middle row).

We consider a host shift to be the inclusion of a novel host in the herbivore's diet, regardless if the herbivore continues to use the ancestral host or not (sensu Agosta 2006, sometimes termed a diet breadth expansion). We searched for papers that tested herbivore host shifts using both top-down and bottom-up forces with Web of Science® on March 29 and 30, 2017, and used combinations of search terms including: enemy-free space, host shift, host expansion, host race, host switch, insect herbivor*, natural enem*, and tri-trophic. We only used
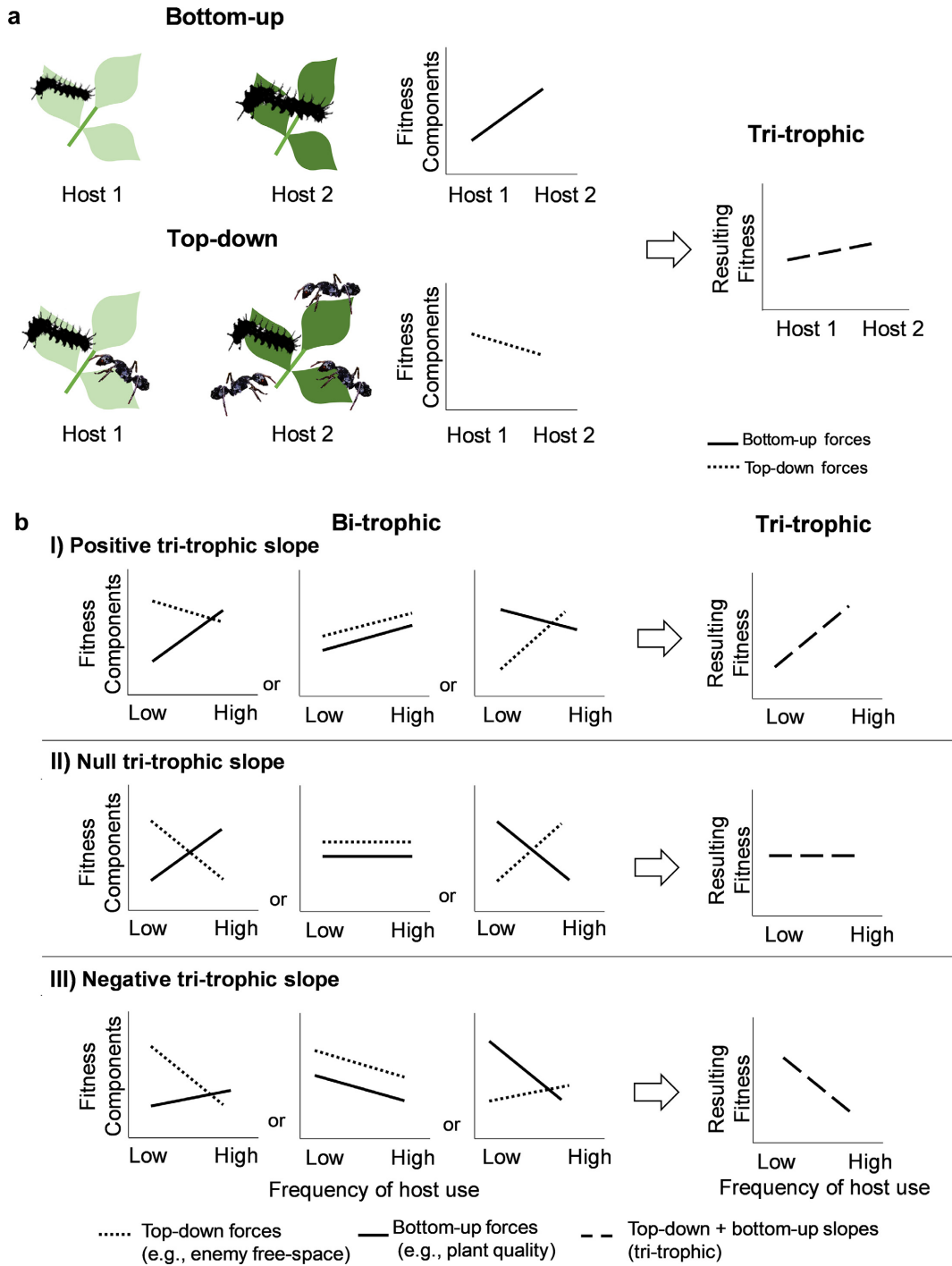
FIG. 1. Conceptual framework of tri-trophic fitness as a relationship between a measure of host plant use (e.g., two hosts or frequency of host plant use) and fitness: (a) Example of a positive tri-trophic fitness. An herbivore has two potential host plants. Host 1 (light green) is of lower quality than host 2 (dark green), and as a result the herbivore grows more when feeding on host 2. When plotting the bi-trophic fitness (bottom-up effects) of the herbivore in relation to the two hosts, we find a positive relationship (solid line). However, the herbivore suffers more attacks by natural enemies (e.g. ants) on host 2 than on host 1, so when we plot the bi-trophic fitness (survival from escaping enemies, top-down effects) in relation to the two hosts, we find a negative relationship (dotted line). In this example, there is greater positive difference in bottom-up forces than the negative difference in top-down forces, so the resulting tri-trophic fitness is also positive (dashed line). (b) Conceptual framework of how to measure tri-trophic fitness based on all possible cases of bi-trophic interactions that consider only top-down (TD; e.g. enemy-free space, EFS) or bottom-up (BU; e.g. host plant quality on larval fitness) forces in relation to frequency of host plant use (from low to high). We consider both TD and BU as positive effects on the herbivore. For example, for the BU force lines, high quality host plants result in greater fitness components (e.g. survival) for the herbivore. Similarly, for the TD force lines, host plants where the herbivore escapes enemies (e.g. EFS; the herbivore suffers reduced predation/parasitism) result in greater fitness components (e.g. survival) for the herbivore. In the bi-trophic figures, TD or BU selective forces are shown separately with respect to frequency of host plant use in a given time. The tri-trophic figures show the separate bi-trophic slopes added together (similar as the mean of bi-trophic fitness components); the direction of the

(Fig. 1. *Continued*)
tri-trophic slope is similar (positive, null, or negative) if fitness components are multiplicative (top-down fitness as a portion of bottom-up fitness, not shown here). Considering tri-trophic fitness, we have three possible scenarios: I) TD, BU or both are significantly greater for the most frequently used host resulting in positive tri-trophic fitness; II) TD and BU cancel each other, or there is no difference among hosts; III) the host plant most frequently used is associated with lower TD and/or BU effects, resulting in negative slope of the tri-trophic interaction.

TABLE 1. Summary of the data collected from published papers testing host shifts by herbivorous insects for both naturally occurring and artificial host shifts (by increasing tri-trophic result).

Paper	Naturally occurring host shift?	Herbivore	Ancestral host	Novel host(s)	BU change	TD change	Tri-trophic result
Gross et al. (2004a,b)	N (this population)	*Chrysomela lapponica*	*Salix borealis*	*Betula pubescens*	−0.84	0.1	−0.74
Gratton and Welter (1998, 1999)	N	*Liriomyza helianthi*	*Helianthus annuus*	*Centaurea solstitialis*	−0.25	0.14	−0.11
Mira and Bernays (2002)	Y	*Manduca sexta*	*Datura wrightii*	*Proboscidea parviflora*	−0.45	0.43	−0.02
Vosteen et al. (2016)	Y	*Acyrthosiphon pisum*	*Vicia faba*	*Trifolium pratense*	−0.1	0.2	0.10
				Pisum sativum	0	0.07	0.07
				Medicago sativa	−0.38	0.74	0.36
Murphy (2004)	Y	*Papilio machaon*	*Cnidium cnidiifolium*	*Artemisia arctica, Petasides frigidus*	−0.22	0.29	0.07
Feder (1995), Prokopy et al. (1988)	Y	*Rhagoletis pomonella*	*Crataegus* spp. (hawthorn)	*Malus pumila* (apple)	−0.25	0.32	0.08
Diamond and Kingsolver (2010)	Y	*Manduca sexta*	*Nicotiana tabacum*	*Proboscidea lousianica*	−0.29	0.4	0.11
Mulatu et al. (2004)	Y	*Phthorimaea operculella*	*Solanum tuberosum* (potato)	*S. lycopersicum* (tomato, all 3)	−0.13	0.27	0.14
Brown et al. (1995)	N	*Eurosta solidaginis*	*Solidago altissima*	*S. gigantea*	−0.14	0.32	0.18
Meijer et al. (2016)	Y	*Rhagoletis alternata*	*Rosa canina*	*R. rugosa*	0.23	0.06	0.29
Torres-Vila and Rodríguez-Molina (2013)	Y	*Lobesia botrana*	*Daphne gnidium*	*Vitis vinifera*	0.69	0.04	0.73

papers that had clear novel and ancestral hosts and had direct measures of bottom-up and top-down effects on both hosts. With these criteria, we found 14 papers (13 cases) for our analysis that ranged from 1988 to 2016 (Table 1). Appendix S1 has details on data extraction of each paper. In this first test, we only have two categories on the *x*-axis, thus we calculate the bi-trophic measures as the difference in fitness between novel and ancestral hosts. We added the differences in fitness to derive the resulting tri-trophic fitness. We used a binomial test (Siegel and Castellan 1988) with a correction for small sample sizes to test if the number of cases with positive or null resulting tri-trophic fitness supported our hypothesis. We deposited our data from tests I and II in the Dryad Digital Repository (see Data Availability; Vidal and Murphy 2018b).

Test II – Case study using populations of a generalist herbivore with variable diet breadth

For the second test of our approach, we present a case study in which we used the tri-trophic fitness slope to interpret and predict diet breadth evolution of a generalist herbivore. Fall webworm (*Hyphantria cunea*, Erebidae, Lepidoptera; hereafter FW) is an insect herbivore native to North America and is a dietary generalist that feeds on more than 600 host plant species over its geographic range (Warren

and Tadic 1970). As a species, FW are dietary generalists, but individual larvae feed only on the plant species upon which their mother oviposited. FW is a great model organism to study diet specialization because the diet breadth of populations varies considerably across their geographic range (e.g. Mason et al. 2011, Murphy and Loewy 2015). We investigate why some populations are more specialized or generalized than others; for a species like FW that is a true generalist and seems to remain so over time, we predict that the maintenance of generalism would require populations that are more generalized in their diet breadth to have greater fitness associated with tri-trophic interactions than populations that are more specialized in their diet breadth. If populations that are more generalized in their diet breadth have lower fitness associated with tri-trophic interactions than populations that are more specialized, then dietary generalism would not be maintained at the species level and FW would become a dietary specialist. In the case of fitness slopes, we would expect generalist populations to have positive slopes, which would show that these populations are well adapted to the many hosts they use most frequently. In our model, we use mean fitness for individuals within a population and diet breadth at the population level because FW feed during their entire larval stage on only one host plant individual, and thus we cannot calculate individual diet breadths.

To analyze how spatial difference in strength of bottom-up and top-down forces influences diet breadth, we sampled 10 different populations of FW in Colorado in the summers of 2011–2012 (data from Murphy and Loewy 2015) as well as 2014–2016. We considered the 10 sampling locations as different populations because female FW are known to not fly far from their emergence location and males can fly up to 23 km (Yamanaka et al. 2001), a smaller distance than our two nearest locations (48 km). Female moths lay eggs in a clutch on a single host plant and sibling larvae feed in aggregation, forming a web that encompasses the host plant branches, usually including hundreds of sibling larvae. In each population, we looked for webs near roads and rivers where FW usually occur and we sampled the webs following the transect methods used by Murphy and Loewy (2015). We sampled at least 21 webs in each population, and we collected 10 larvae from each web to rear in our laboratory to measure percent parasitism, pupal mass, and survival. In the laboratory, we fed all larvae with leaves from the same host plant species collected from the location from which the larvae were found. We used the same protocol for data collection and larval rearing as Murphy and Loewy (2015) and thus were able to include data from Boulder, Larimer and Jefferson populations from that study.

We used the product of the mean pupal mass and proportion survival on a plant species within each population as a measure of bottom-up forces, and percentage of larvae that escaped parasitoids (not considering larvae that died from other causes) as a measure of top-down forces. Pupal mass and survival are fitness measures related to plant quality (Awmack and Leather 2002); larvae reared on plants considered of high quality have greater survival and greater pupal mass than larvae reared on poor quality hosts, and since pupal mass is directly related to lifetime fecundity, it is a reliable fitness proxy (Loewy et al. 2013). FW larvae are greatly affected by parasitoids and are less affected by invertebrate and bird predation (Morris 1972, 1976), therefore parasitism rate is a reliable measure of the strength of top-down forces. We collected FW during all developmental stages at all of our sites (except Baca, but see below) so as to accurately assess parasitism by both early season (generally wasps) and late season (generally flies) parasitoids (Murphy et al. 2014). Plant abundance has been shown to influence host plant use by FW (Mason et al. 2011, Murphy and Loewy 2015), therefore we tested if frequency of host use was related to abundance of the host. We calculated relative abundance and relative host use following Mason et al. (2011) and Murphy and Loewy (2015), and we analyzed the relationship between host plant use and abundance using linear regression for populations that used three or more host plant species.

To test if pupal mass, survival, and parasitism rates varied among populations and host plant species, we used a (generalized) linear mixed model with pupal mass, survival or parasitism as the response variable, *host plant* and *population* as fixed factors, and the *web of origin* as a random factor. For the models including survival and parasitism rates, we used a binomial distribution. We performed our analyses in R environment 3.4.1 (R Development Core Team 2011), and we used the package *afex* v. 0.18-0 with function *mixed* (Singmann et al. 2017). To calculate each bi-trophic fitness slope, we determined the relationship between the fitness measure for each host plant species with respect to frequency of host plant use for each population. Then, we used the additive result of the two bi-trophic slopes as the tri-trophic fitness relationship among host plants for each population. We used two continuous measures of diet breadth: (1) the number of plant species included in the diet of each population, and (2) Ordinated Diet Breadth (ODB), which calculates diet breadth relative to the identity of plants used in each population compared to the hosts used by other populations (Fordyce et al. 2016). With ODB, when a population uses more plants that are dissimilar to those used by another population, it gets a higher diet score (Fordyce et al. 2016). The number of hosts used and ODB is expected to be correlated but may differ from each other if, for example, an herbivore with narrow diet breadth (considering number of plant species) uses completely different host plants than the other herbivores; the ODB would then suggest that that herbivore has a diverse diet (Fordyce et al. 2016). We used the package *ordiBreadth* to calculate ODB in R. We analyzed how tri-trophic fitness slope influences diet breadth by using a linear regression.

One limitation of our approach is that we do not have a measure of variance associated with the tri-trophic slopes. To test if our approach is reliable, we compared our result using the addition of bi-trophic slopes with results from linear models using mean and standard deviation obtained from resampling and from Bayesian linear regression. Considering the resampling technique, for each population, we obtained all possible bi-trophic slopes from pairwise combinations of host plants included in our frequency of host plant use by bi-trophic fitness relationship for that population. Using those pairwise-slopes, we resampled 1,000 slopes using the function *resample* in R, from which we calculated the mean and standard deviation. For the Bayesian linear regression, we calculated mean and standard error of slopes based on a Bayesian regression with non-informative priors between the frequency of host plant use and bi-trophic fitness measures (both top-down and bottom-up) for each population. We first used the *lm* function to obtain a standard linear model using bi-trophic fitness as the response variable and frequency of host plant use as the fixed effect, and from this model, we extracted coefficients, degrees of freedom and variance matrix to calculate the mean and standard error using Monte Carlo integration with 10,000 iterations. A similar result obtained with these different methods would demonstrate that the tri-trophic slope approach is reliable.

Another limitation of our tri-trophic slope approach is that we use an additive effect when comparing slopes, and one could argue that the relationship between top-down and bottom-up forces should be represented as multiplicative. To show that our approach yields similar trends as a multiplicative approach, we performed another analysis with a multiplicative measure of fitness associated with tri-trophic interactions, which we refer as "tri-trophic score". In each population, we obtained the mean pupal mass per host plant species and multiplied it by the proportion of survival from escaping natural enemies on the same host species (without considering mortality by other factors). Since this measure does not take into consideration the frequency of host plant use as our tri-trophic slope does, we used another measure of diet breadth that included this frequency, the Shannon-Weiner Diversity Index (H'). To calculate the diversity of diet breadth in each population, we summed the product of

proportion of use and *natural log of the proportion* for all hosts used in each location; therefore, we considered both the number of plants used and the frequency by which they were used, which is thus a measure of the herbivore's diet diversity (and not plant community diversity). To make this value meaningful, we exponentiated the H' as proposed by Jost (2006), and tested the correlation between diet diversity and tri-trophic score using *lm* in R.

RESULTS

Test I – Proof of concept using host shifts by multiple insect herbivore taxa

As predicted, we found that all cases of host shift in which the herbivore used the novel host in nature had a positive or null tri-trophic fitness (Table 1). Of the 13 cases, 10 had a positive tri-trophic fitness on the novel host compared to the ancestral host, one had a null tri-trophic fitness (−0.02 in Table 1) and two had negative tri-trophic fitness (Table 1, −0.1 and −0.74); these results support our hypothesis that herbivores shifting to novel hosts have a positive or null resulting tri-trophic fitness (binomial test, N = 13, k = 2, P = 0.011) Considering the two cases with negative resulting tri-trophic fitness, one was from an experimental host shift in which the insect was switched to a plant it would not use naturally (Gratton and Welter 1999), while the other was from a population that did not experience a host shift (Gross et al. 2004a,b). Both top-down and bottom-up differences in fitness had a significant relationship with tri-trophic fitness (r^2 = 0.57, P = 0.003 and r^2 = 0.7, P = 0.0004, respectively); thus, there was no specific bi-trophic difference that drove the pattern of tri-trophic fitness. Interestingly, all cases had a positive top-down difference in fitness, which shows that the herbivores suffered lower attack from natural enemies on the novel host. Most of the cases had a negative bottom-up difference in fitness, except for two that were positive and one that was null. Thus for 10 of the 13 cases we found trade-offs between top-down and bottom-up forces (positive top-down and negative bottom-up).

Test II – Case study using populations of a generalist herbivore with variable diet breadth

We found significant variation across all populations and across hosts for parasitism rate (Population: X^2 = 60.47, df = 9, P < 0.0001, Host: X^2 = 55.56, df = 29, P = 0.002), for pupal mass (Population: $F_{9,376.23}$ = 3.76, P = 0.0001, Host: $F_{29,435.56}$ = 1.63, P = 0.02), and for survival rate (Population: X^2 = 52.36, df = 9, P < 0.0001, Host: X^2 = 43.2, df = 29, P = 0.04). The variation in plant quality and parasitoid pressure fits well with the conditions of our model, as we need to have variation in selective pressure among populations to be able to compare the effect of variation in tri-trophic fitness on different diet breadths. There is a correlation between abundance and frequency of host use for all populations (r^2 values range from 0.38 to 0.89, all P < 0.05), as was also found by Murphy and Loewy (2015) and Mason et al. (2011). This correlation was mainly driven by the most frequently used host; when we removed the host most frequently used, we found no relationship between host use and abundance (similar to Murphy and Loewy 2015). Only two populations had negative

bottom-up slopes (triangles in Fig. 2a), while two populations had positive top-down slope (open circles in Fig. 2a). This means that most populations fed most frequently on better quality hosts, but those were host plants associated with higher parasitism rate (see Appendix S2 for bi-trophic slopes, host abundance and host use).

Considering the combined effects of different bottom-up and top-down forces on diet breadth of FW, we found a positive correlation between tri-trophic slopes and both the number of plants used and ODB (plant number: r^2 = 0.6, P = 0.008; ODB: r^2 = 0.57, P = 0.012; Fig. 2a, only ODB shown because figures were nearly identical for the two measures), in which populations with positive slopes had a broader diet, while populations with negative slopes had narrower diet. The pattern was maintained when we removed Baca, which was the site where we were unable to collect all developmental stages, but only remained significant for number of plants used (for ODB: r^2 = 0.39, P = 0.11). Using mean of slopes from resampling and Bayesian linear regression, we found a positive correlation between ODB and mean slopes in both cases (resampling: Fig. 2b, r^2 = 0.43, P = 0.04; Bayesian: Fig. 2c; r^2 = 0.56, P = 0.013). Using these methods, our slopes had high values of variation, however, this should be expected as we are simplifying a huge dataset into one informative measure. The tri-trophic fitness slope obtained with our approach is positively correlated with the mean slope obtained with Bayesian regression (r^2 = 0.99, P < 0.0001), and with resampling (r^2 = 0.48, P = 0.026). Lastly, when we considered the correlation between diet breadth diversity and tri-trophic score, we found that FW populations that had higher "tri-trophic fitness" had more diverse diets (Fig. 2d, r^2 = 0.09, P = 0.006).

We found four populations with a negative tri-trophic fitness slope (i.e., individuals feed more frequently on the host(s) associated with lower tri-trophic fitness), and six with positive tri-trophic slope (i.e., individuals feed more frequently on the host(s) associated with greater tri-trophic fitness). There was a positive relationship between the number of webs sampled and number of plants used (r^2 = 0.46, P = 0.03), but there was no relationship between sample size and tri-trophic slope (r^2 = 0.19, P = 0.2). Bottom-up slope was positively correlated with tri-trophic slope (r^2 = 0.96, P < 0.0001), but top-down was not (r^2 = 0.31, P = 0.1). Therefore, in this case tri-trophic fitness might be driven by bottom-up forces.

DISCUSSION

Assessments of tri-trophic effects on herbivore fitness have been done qualitatively by inferring the combined effect of quantitative measures of bottom-up and top-down forces on herbivore fitness (e.g. Murphy 2004). However, the quantitative resulting effect of those two selective forces can differ from just qualitative comparisons. Here, we propose a way to quantitatively measure tri-trophic effects on herbivore fitness by adding the bi-trophic fitness slopes to integrate the relationship between variation in selective forces and a measure of host plant use. We found that studies testing naturally occurring host shifts had greater tri-trophic fitness on the novel hosts than on the ancestral hosts, as we predicted. Further, we showed that for a generalist herbivore (FW), the tri-trophic fitness slope is positively correlated with diet breadth:
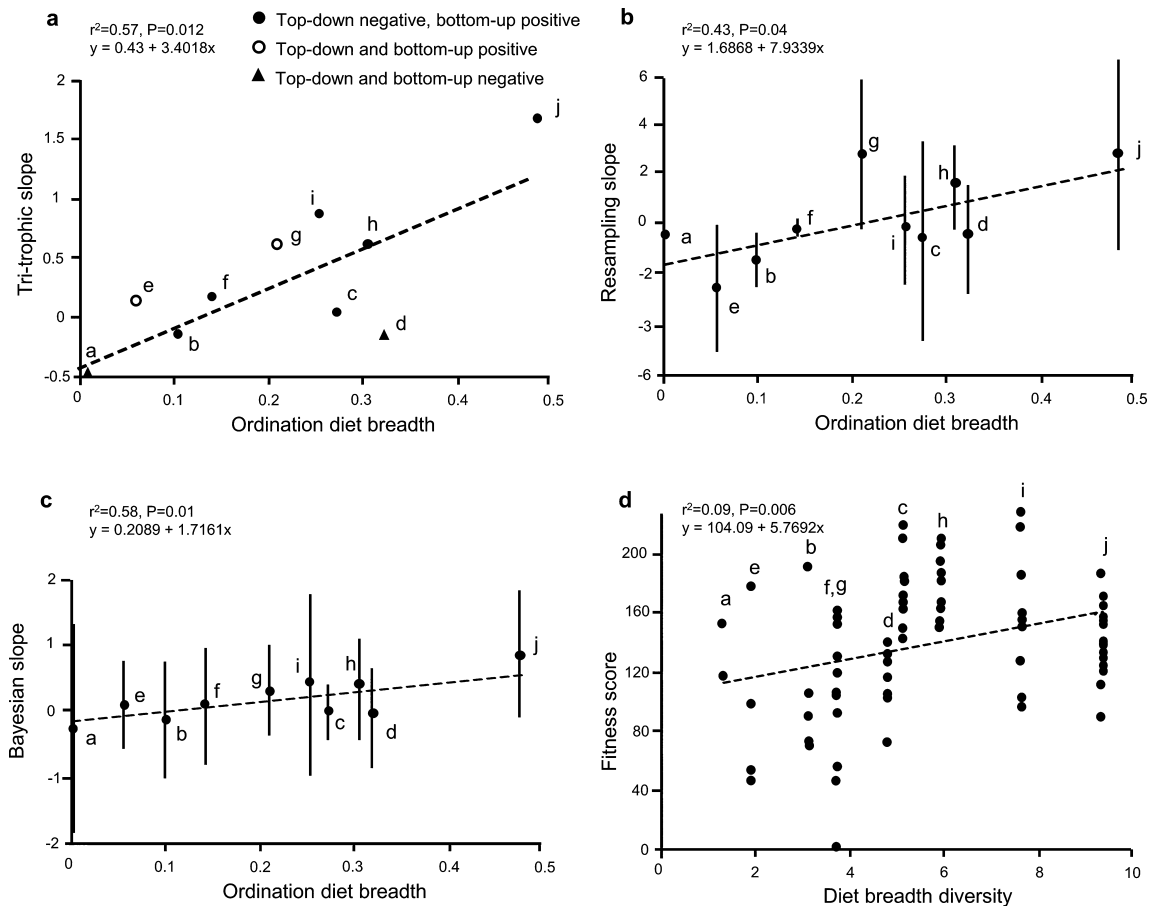
FIG. 2.   Relationship between diet breadth and measures of fitness associated with tri-trophic interactions for fall webworm populations. (a) Diet breadth measured using Ordinated Diet Breadth (ODB, Fordyce et al. 2016) and fitness measured as the resulting tri-trophic slope as explained in Fig. 1; circles represent populations with positive bottom-up slope and triangles represent populations with negative bottom-up slope, open circles represent positive top-down slopes. (b) Diet breadth measured using ODB and fitness measured as mean of pairwise top-down and bottom-up slopes from resampling, lines represent standard deviation. (c) Diet breadth measured using ODB and fitness measured as mean of the regression between frequency of host use and bi-trophic fitness (both bottom-up and top-down) obtained by Bayesian linear regression, lines represent standard error. (d) Diet breadth diversity measured as exponential of Shannon-Wiener Diversity index and fitness measured as the multiplication of pupal mass and proportion survival from natural enemies (i.e., Fitness score). Each data point is a different population for graphs (a–c), while for graph (d) each point is the fitness measure on a host plant for each population. Letters represent the county where the population was located in Colorado: a – Arapahoe, b – Las Animas, c – Jefferson, d – Mesa, e – Garfield, f – El Paso, g – Chaffee, h – Baca, i – Larimer, j – Boulder.

populations using a greater number of different plants (i.e., generalists) have greater fitness associated with tri-trophic interactions on the plants that the individuals use more frequently. Our quantitative measure of fitness associated with tri-trophic interactions will allow us to better understand why and how diet breadth of herbivores change over space and make predictions of how natural populations of a generalist herbivore might change their diet breadth over time. Assuming that natural selection is acting on the individuals of a population, selection should favor individuals that have greater tri-trophic fitness on specific hosts, which would lead to a change in the pattern of host plant use according to the tri-trophic fitness in each population. In the case of a generalist herbivore such as FW, our finding suggests that generalism is maintained because there is clear fitness advantage of having a broader than a narrower diet for the populations of this species (i.e., Fig. 2d). This gives further support to the idea that being a generalist is not necessarily a disadvantageous strategy (Vidal and Murphy 2018*a*).

Our tests considered only a snapshot of the tri-trophic slopes and diet breadths in a specific time. As selective forces are expected to vary over time (e.g., Heard et al. 2006), our tri-trophic slope is not stable in time. For example, we would expect that populations with a steep positive slope that are generalists (letters *j* and *i* in Fig. 2a) would eventually stop using the hosts that they use in low frequency and on which herbivores have low tri-trophic fitness (top-down fitness is high, but bottom-up fitness is very low). Those populations may therefore use fewer hosts and thus their tri-trophic slope may become closer to zero because as the low-frequency hosts are eliminated from the diet, the diet would include only the formerly medium-frequency and the high-frequency hosts with tri-trophic fitness more similar to each other. Alternatively, if the selective advantage of enemy-free space is great enough, there may be selection for individuals that perform well on the low-quality host plants. Murphy (2004) suggested that enemy-free space should be ephemeral because selection for improved physiological performance on low-quality hosts

should be high if the relief from natural enemies is great enough. Thus, the bi-trophic bottom-up slope would become less steep as low-frequency host plants became higher-quality and the tri-trophic slope would also decrease (approach zero). On the other hand, the populations with negative tri-trophic slopes represent those with a maladaptive diet (when considering only top-down and bottom-up forces). Unless gene flow with populations with different ecological conditions maintains these patterns, the negative slopes could change over time as larvae with greater performance would be selected for on the plants they use in high frequency, or frequency of host use would change. Overall, we would expect that over time populations would move along the dashed regression line in Fig. 2, "sliding" from the lower left to the upper right or vice versa, which would correspond to selection for intermediate to broad diet breadths for this dietary generalist. We highlight that we refer to "specialist" and "generalist" populations of FW, but these terms are relative as all FW are still considered generalists and even some "specialist" FW populations feed on more than three host plant species (following Bernays and Graham 1988). Thus, an intermediate diet breadth for FW is still highly generalized compared to most insect herbivores.

We found that trade-offs between top-down and bottom-up forces can be very common. Indeed, for our host shift analysis of published studies, we found trade-offs for 10 of the 13 cases; changes in bottom-up fitness were mostly negative and in top-down were all positive. Interestingly, we found positive or null tri-trophic fitness changes for all cases in which the shift was a naturally occurring host shift by the herbivore. This gives support to the idea that specialist herbivores include new hosts in their diet when the host is advantageous, and in these cases the benefit of escaping enemies on the new host trumps the disadvantage of the novel hosts being of worse bottom-up quality. For our FW data, the majority of populations had positive bottom-up slopes and negative top-down slopes (Fig. 2a, filled circles). This result suggests that FW feeding on infrequently used host plants may escape their enemies, and thus that these infrequently used host plants may offer enemy-free space. Another possibility is that parasitoids are preferentially attacking herbivores on hosts that are used more frequently (as host plant dependent parasitism, e.g., Lill et al. 2002, or density-dependent parasitism, e.g., Singer et al. 2012).

Our model to calculate tri-trophic fitness can be helpful to interpret pattern amidst many data points. In our model FW system, we had almost 4,000 data points (individual FW larvae feeding on different host plants across sites), and great variation in bi-trophic forces within and across populations and host plants. We could more clearly see this variation when we used Bayesian regression and resampling to calculate the tri-trophic slopes. Yet, using tri-trophic fitness slopes, the pattern for each population became clear and we could infer how selective forces influenced diet breadth. Although selective forces are expected to vary in strength over time and space, few papers on top-down and bottom-up forces have adopted this view (Gripenberg and Roslin 2007, but see Heard et al. 2006). Notably, our study uses a geographic mosaic of selection (Thompson 2005) to investigate diet breadth evolution, which together with our tri-trophic fitness slope approach, can be used to better understand diet breadth evolution and what leads some populations to have

broader diet than others depending on their local selective forces. Furthermore, we showed that our quantitative measure of fitness works well with other systems given that we obtained the expected pattern with host shift data.

Top-down and bottom-up forces are not independent from each other. For example, host plants can mediate herbivore-natural enemy interaction (e.g., Lill et al. 2002) and inter predator interactions can influence host plant-herbivore interactions (e.g., Mira and Bernays 2002). However, most studies of plant-insect interactions still test bottom-up and top-down selective forces separately and we believe that having a method to consider the fitness measure resulting from the combined top-down and bottom-up interactions (i.e., our tri-trophic fitness) is a step forward in the way we currently analyze tri-trophic interactions. We believe that our tri-trophic slope approach will be useful in future research testing top-down and bottom-up effects in herbivore-plant interactions.

Limitations, potential applications, and concluding remarks

Our approach is a first step towards a quantitative measure of fitness associated with tri-trophic interactions or multiple selective forces. Due to its simplicity, the approach has a few limitations that can be potentially explored in future research. One of the limitations is that we assume a linear relationship between fitness and a measure of host use, which is not necessarily true. In the case of only two levels for the x-axis, the linear relationship will be supported, as was the case with our first test using published data on host shifts. However, in our second test, we had many data points for most of the FW populations, and even though in most cases the relationship between fitness and host use was linear, there were some cases in which the intermediate-frequency host would be the best host. The calculations using non-linear relationships are more difficult, but they are still possible and can be used to make predictions (e.g. mutualism dynamics Holland and DeAngelis 2010). A good starting point would be to find out the best fit of one's data, for example, by using generalized additive models (Zuur et al. 2009). Another limitation is that we assume an additive effect of bi-trophic slopes, which is not always the case. This limitation is easy to deal with if the system of study and the responses to the different selective forces are well known. For example, in the risk allocation hypothesis, it is expected that prey response will depend on both the level of risk and the amount of time that predators are present (Lima and Bednekoff 1999). However, the effect of the level of risk and exposure time is not additive, as extremes in both risk and exposure can lead to weak prey response (Ferrari et al. 2009).

An additional limitation is that our approach does not directly consider variation in the data. This again might be a problem with multiple data points, as the line will consider the entire distribution of points, but may not necessarily be a good fit. However, we showed that it is possible to get a measure of variance using either a resampling or Bayesian approach, but these approaches are more technical and not always user-friendly. Our approach of combining slopes is both easier and yields similar results, and our results were correlated with those of the Bayesian and resampling results. In the case of only two categories of dependent variable, as we have in our test 1, this problem can be easily dealt with if

we use the raw data. Using Fig. 1a as an example, suppose that individuals from the same genotype are reared on host A and B, the difference in fitness associated with top-down and bottom-up forces could be calculated for all genotypes and then add these values to get the tri-trophic fitness. That would result in multiple values of tri-trophic fitness, and one could use the mean and standard deviation. In our case, we unfortunately did not have access to the raw data, as we collected the data summary from published host shift studies, many of which do not report variance (see Vidal and Murphy 2018a for a discussion of how ecologists often do not report variance in top-down measures).

Problems may result when the fitness measures differ between the two selective forces. It is advisable to use similar ranges to measure bi-trophic fitness slopes. In our test 2, we used survival for top-down forces that usually ranged from 50 to 100, and we considered the multiplication of proportion survival by pupal mass as our bottom-up force, which ranged from 30 to 160. It is still a similar range, however, we found that bottom-up forces were the main driver of tri-trophic slopes, which might be because of it having a broader range. One way to deal with this problem is to use the log of the slopes to get a similar value between them; we tried this approach with our data, and we found a similar trend as with the raw data (but it was only marginally significant). If there is more than one fitness measure per selective force, one can also use eigenvalues from principal component analysis, given that the vectors used explain a good portion of the data. But we advise that thought should be put into what fitness measure to use before conducting an experiment, as the fitness proxy used should be well connected to the fitness of the study organism and to make calculations easier.

Theme	Example of problems	Example of application	Example of conceptual framework
Niche specialization	(1) Competition leads to niche specialization; (2) Top-down and bottom-up forces (or other selective forces) lead to expansion or retraction of niche.	(1) Competition for resources might lead to niche specialization or contraction[1]. If the resulting fitness slope from the fitness with or without competing species is negative (as in example), then niche specialization is expected. While if it is null or positive, niche expansion is expected.	
Mutualistic interactions	(1) Mutualism and antagonism interface; (2) Maintenance of mutualism over time.	(1) Facultative mutualisms are context dependent and might become antagonistic when one of the partners is harmed[2]. If the resulting slope is null or negative, partners have higher fitness outside the mutualism which would exemplify antagonism, whether if it is positive, might be a mutualistic interaction (as example). The steepness of the slope can also inform about the asymmetry of the relationship. In the example, Partner 2 might depend more on the interaction than Partner 1, as the latter has almost a null slope.	
Sexual vs. Natural selection	Which selective force drives the trait evolution.	Natural and sexual selection acting in opposite ways can lead to genetic variation in traits[3]. If the resulting slope of the two selective forces is null, then high genetic variation (or trait variation) is expected (as in example). While if it is positive or negative, one of the selective forces is stronger and thus driving selection, leading to directional selection of that particular trait.	

FIG. 3. Examples of possible applications of our conceptual framework. [1]Futuyma and Moreno (1988), [2]Chamberlain et al. (2014), [3]Gray and Cade (1999).

Other studies have integrated multiple measures by multiplying the fitness components within each category being compared (e.g., Murphy and Loewy 2015 "fitness score"), which seems to be a viable method and we showed that it yields similar results as our approach (Fig. 2d). Another possibility would be to use one measure of fitness under both bottom-up and top-down selective forces simultaneously and use linear models with bottom-up and top-down forces as fixed effects to predict fitness outcomes. However, we as ecologists tend to measure top-down and bottom-up forces separately, or use different fitness measures associated with each, which would make traditional linear model approaches difficult to use. A good example of how to get a combined measure from multiple effects is the one used in multiplicative predator risk studies (Sih et al. 1998). Researchers multiply the predation rate from each predator measured separately to estimate the possible combined effect of multiple predators on the prey (Soluk and Collins 1988). Multiplication of fitness effects seem to be an effective way to combine multiple measures, and we showed that our approach using the addition of slopes yields similar results.

One of the challenges in ecology and evolution is to find pattern in the initial chaos that may appear when natural communities are first examined. In an attempt to study these patterns, we as ecologists and evolutionary biologists tend to simplify possible interactions and selective forces to interpret one or a few at a time, such as the many studies that focus only on bi-trophic interactions when we now know that insect herbivore-plant interactions can only be interpreted in a tritrophic (or multi-trophic) context (Vidal and Murphy 2018a). Since our framework is simple and straightforward, there are many options of applications and modifications that can be made, and here we suggest only a few. Any research question that has measures of two selective forces in similar conditions can use our framework to obtain the resulting effect of these two forces together. For example, we envision applications for questions of niche specialization, mutualistic interactions or tests of sexual vs. natural selection (Fig. 3). Our conceptual framework is a first step towards a more complex integration of multiple selective forces, in which we intend to analyze the fitness consequence of at least two selective forces acting together on the focal organism. We believe that our conceptual framework can open possibilities for the development of more complex frameworks and can be applied to studies that measure multiple selective forces to understand the evolution of interactions.

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SUPPORTING INFORMATION

DATA AVAILABILITY