

ARTICLE

Bottom-up and top-down pressures mediate competition between two generalist insects

Elizabeth E. Barnes  | Shannon M. Murphy 

Department of Biological Sciences,
University of Denver, Denver,
Colorado, USA

Correspondence

Elizabeth E. Barnes
Email: barnes.elizabeth20@gmail.com

Present address

Elizabeth E. Barnes, Department of
Entomology, Purdue University, West
Lafayette, Indiana, USA.

Funding information

Boulder County Parks and Open Space;
Jefferson County Open Space; Sigma Xi;
University of Denver Shubert Award

Handling Editor: Julian Resasco

Abstract

The effects of competition can have far-reaching consequences for individuals, populations, and communities and therefore we should strive toward a deeper understanding of competitive interactions. In some cases, dietary generalists may be predicted to experience weak competition effects because of their ability to use a wide range of host plants. However, competition between insects frequently occurs indirectly, which can hinder insects' abilities to avoid competitive interactions. Therefore, competition may be as strong among dietary generalists as among dietary specialists. Yet competition between insects that are dietary generalists is infrequently studied. We tested for evidence of competitive interactions between two common, temporally separated, generalist insects: the western tent caterpillar (*Malacosoma californicum*), which feeds early in the season, and the fall webworm (*Hyphantria cunea*), which feeds later in the season. Both species frequently use a common host plant species (chokecherry) as a preferred host at our field sites. We tested the relative strength of bottom-up effects resulting from competitive interactions between these two generalists with laboratory-rearing trials at the relevant time of year for each insect. We recorded three common fitness measures (development time, pupal mass, and survival) for caterpillars reared on chokecherry with no damage from either of our focal species, with tent caterpillar damage, and with fall webworm damage. To test the strength of top-down pressures on fall webworm larval fitness and any potential interactions with bottom-up effects, we reared larvae in the field either exposed to or protected from predators on host plants that either did or did not have tent caterpillars feeding on them earlier in the season. We found evidence of bottom-up fitness effects on tent caterpillars and top-down and bottom-up fitness effects on fall webworms confirming that tent caterpillars and fall webworms compete indirectly. Tent caterpillars had lower pupal mass when reared on leaves from shrubs damaged by fall webworms. Fall webworms had lower pupal mass and longer development time when reared on leaves from shrubs damaged by tent caterpillars. In field trials, fall webworms reared on shrubs damaged by tent caterpillars had a lower survival and pupal mass. We show evidence of indirect competition in temporally separated generalists through leaf quality (bottom-up effects) and natural enemies (top-down effects).

KEYWORDS

bottom-up pressures, dietary generalists, fall webworm, *Hyphantria cunea*, indirect competition, Lepidoptera, *Malacosoma californicum*, *Prunus virginiana*, tent caterpillar, top-down pressures

INTRODUCTION

Competition can play a key role in a range of ecological processes from population cycles to host plant use to speciation. For example, in insects, there are documented instances of competition driving host shifts when the negative fitness impacts of competitors outweigh the benefits of an otherwise high-quality host (Janzen, 1973; Tuda et al., 2014). Higher competitive ability in dietary specialists has been suggested as an explanation for the greater diversity of dietary specialists than generalist insects, but this prediction was contradicted by a recent meta-analysis that found an equal frequency of competition in specialists and generalists (Bird et al., 2019). The findings of this meta-analysis are surprising, because dietary generalists are able to use a wide range of host plants and might be expected to choose plants where they would experience lower levels of competition (e.g., Dittrich & Helden, 2020). However, in herbivorous insects, indirect competition mediated by a third organism is more common than direct competition (Kaplan & Denno, 2007) and competitors may not even be present on the host plant at the same time. This type of competition can make it more difficult to assess the cues that insects might otherwise use to choose a host plant with lower levels of competition because the competitors are not present and signs of their presence may have disappeared. Studies that focus explicitly on the interactions of dietary generalists are needed if we are to understand if, how, and when these insects impact each other's fitness and decisions related to host plant selection. We therefore conducted multiple experiments testing the indirect competitive effects between two common and widespread generalist herbivores, the fall webworm (*Hyphantria cunea* Drury, Lepidoptera: Erebididae) and tent caterpillars (*Malacosoma californicum* Packard, Lepidoptera: Lasiocampidae).

At present, the literature on generalist–generalist competition is limited in scope. Despite the potential for variation in how competition affects specialists and generalists, most research on competition among herbivorous insects focuses on dietary specialists and those studies that do include generalists tend to rear them on agricultural crops. Of the papers considered in a meta-analysis of insect competition (Kaplan & Denno, 2007), only 10% of the pairs of competing species

(some papers included multiple pairs of species) included in the meta-analysis tested two competing generalists and, of those, half (54%; ~5% of total studies) were tested on agricultural host plants, which are often grown in monocultures that are likely to alter insect behavior (Klapwijk & Björkman, 2018; Shi et al., 2014; Wang et al., 2019). Agricultural monocultures lack alternate hosts for the insects to shift to as a means of lessening competition, which may increase the intensity of competition. Therefore, we do not expect competition among dietary generalists in agricultural settings to resemble competition between dietary generalists in natural areas.

Competition occurs indirectly through bottom-up (e.g., plant secondary compounds, leaf toughness, etc.; e.g., Bezemer et al., 2003; Faeth, 1986; Redman & Scriber, 2000; van Dam et al., 2005) and/or top-down pressures (e.g., predation, parasitism, etc.; e.g., Jeffries & Lawton, 1984; Morris et al., 2005; Shiojiri et al., 2002). These indirect effects can cause differences in resource quality among host plants that subsequently can affect herbivore fitness, even when there appears to be a sufficient quantity of resources available (Awmack & Leather, 2002). Plant defenses can act as feeding deterrents, decrease feeding rate, and decrease food-processing efficiency for herbivores (Rasmann et al., 2012). Some of these defenses are constantly present in the plant, but induced defenses are only produced following herbivore damage and may last for a few days to months (Wink, 2010). Short-lived induced responses to herbivory only affect competition between insects feeding on the plant while the damage is occurring, but long-lived or delayed expression defenses can mediate interactions between herbivores that are not necessarily alive at the same time (Faeth, 1986). The long life of some defensive responses means that interactions between herbivorous insects are often temporally separated (Kaplan & Denno, 2007). Thus, insects do not need to feed on a host plant at the same time, or even in the same year, in order to have strong fitness impacts on each other.

Although plants often produce defenses in response to herbivore damage (e.g., Agrawal, 2000; McGuire & Johnson, 2006; Zakir et al., 2013), severe damage can weaken a plant to the degree that it is no longer able to defend itself (Nykänen et al., 2004). Severe herbivore damage to a host plant can also weaken its ability to respond to future damage and reduce the number of

defenses with which subsequent herbivores have to contend (Karban & Baldwin, 1997). There have even been documented instances of light herbivory leading to an increase in fitness for other herbivores (Williams & Myers, 1984) or decreasing some fitness measures but increasing others (Sarfranz et al., 2013). Thus, the impact of host plant-mediated competition may vary widely depending on factors like degree and type of damage (Hrabar et al., 2009; Nykänen et al., 2004). This variability in plant response to herbivory means that it is vital to test herbivore responses to different amounts of damage whenever possible when assessing host plant-mediated effects on insects.

Herbivores may indirectly interact with one another by attracting mutual natural enemies (e.g., Jeffries & Lawton, 1984; Morris et al., 2005; Shiojiri et al., 2002). Predators and parasitoids use many kinds of cues to locate their prey. Many natural enemies rely on host plant volatile cues that the plant releases following damage from herbivores (de Rijk et al., 2013; McCormick et al., 2012; Turlings et al., 1995). These cues can be generalized or specific to particular types of damage and insects (McCormick et al., 2012). Natural enemies may also use visual cues like leaf damage to hunt their prey (Heinrich, 1979; Mäntylä et al., 2008). Some species of parasitoids are attracted to caterpillar silk (Waage, 1978) and frass (Stork et al., 2011). In the case of web- and tent-building caterpillars, natural enemies that are already attracted to a plant through herbivore-associated plant volatiles and leaf damage may be even more strongly attracted to the same plant by webs or tents that provide visual and/or chemical cues that indicate the presence of prey. Because the visual and chemical cues of some insects can last long after they have abandoned their host plant, we might expect their cues to amplify the attraction of natural enemies to a host plant if a species that produces similar cues will colonize that plant in the future.

We examined the effect of indirect competition between two dietary generalist herbivores by testing the effects of both bottom-up (plant quality) and top-down (predators and parasitoids) pressures. The dietary generalist Lepidoptera in our study feed on a range of host plants at our field sites, including at least one overlapping species (chokecherry, *Prunus virginiana* L.). Western tent caterpillar larvae feed on their host plant in early spring and pupate in early summer, while fall webworm larvae feed on their host plant in late summer and pupate in the early fall (Figure 1). Using this study system of two generalist herbivores that use the same species of host plant at different times of the year, we addressed three primary questions: (1) Do these common, dietary generalists compete through bottom-up effects despite significant

temporal separation and are these effects dependent on the amount of damage to the host plant? (2) Are there long-lasting physical and chemical changes to the host plant? And (3) Is the fall webworm, the late-season species, impacted indirectly by tent caterpillars, the early-season species, through top-down effects mediated by natural enemies and predators?

METHODS

Study system

We studied western tent caterpillars (hereafter tent caterpillars) and fall webworms in the foothills of the Colorado Rocky Mountains, where they both feed on many species of host plants including chokecherry (*P. virginiana* L.). Tent caterpillars are gregarious, tent-building larvae that emerge early in the spring, disperse in their penultimate instar, and then pupate and eclose in midsummer (Figure 1); the larvae construct dense silk tents that remain on their host plants through the summer and often into the next year (Barnes, personal observation, June, 2014). Tent caterpillars are destructive, but they rarely kill their host plants (Cooke et al., 2012). Tent caterpillars are dietary generalists (Fitzgerald, 1995), but frequently feed on chokecherry, a high-quality host plant, in the foothills of the Rocky Mountains (Barnes et al., 2016). Fall webworms are web-building larvae that also feed gregariously in silk webs built on branches, but their webs are much more ephemeral than tent caterpillar tents and usually disappear by early winter. Feeding damage by fall webworm larvae can leave large sections of their host plant defoliated and covered in a webbing (Barnes, personal observation, June, 2014). Fall webworms overwinter as pupae and emerge in midsummer as adults to oviposit after tent caterpillars have pupated (Wagner, 2005); after the eggs hatch, the larvae quickly form webs on their host plant (Figure 1; Powell & Opler, 2009). Fall webworms are extreme generalists and can be found feeding on more than 400 woody plant species (Wagner, 2005), including chokecherry, which on the eastern slopes of the Rocky Mountains in Colorado is a high-quality host plant (Loewy et al., 2013).

Tent caterpillars and fall webworms co-occur in our study sites and will frequently use the same individual plants in different years (Barnes, personal observation, June, 2014). Some evidence suggests that both tent caterpillars and fall webworms may avoid ovipositing on shrubs with tent caterpillar tents (Barnes & Murphy, 2018; Travis, 2005). This avoidance behavior by fall webworms may suggest that fall webworms and tent caterpillars have indirect negative fitness impacts on each other.

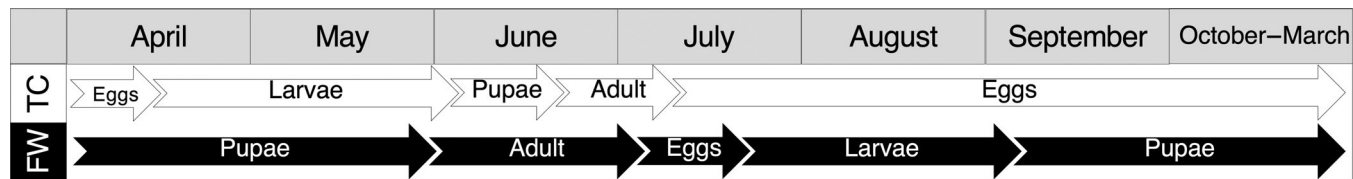


FIGURE 1 A comparison of a typical life cycle of tent caterpillars (TC; white) and fall webworms (FW; black) in the Colorado Rocky Mountains from April to September. Arrows show the time when individuals typically occupy a given stage of the life cycle.

We conducted our experiments along paths, roads, and riparian areas in four sites in Colorado: Betasso Preserve (40°1'28" N, 105°20'19" W), Boulder Canyon Trail (40°0'49" N, 105°18'35" W), Walker Ranch (39°56'36" N, 105°20'56" W), and Centennial Cone Park (39°45'42.3" N, 105°20'32.6" W). Tent caterpillars and fall webworms co-occur and use chokecherry in the same size class (~0.7–2.40 m tall, but most ~1.7 m) at all sites. We tracked the presence and absence of tent caterpillars and fall webworms at each field site on the host plants used in our experiments. All data were analyzed using JMP Pro 16.0.0.

Do fall webworms affect tent caterpillars through bottom-up effects?

We tested if the fitness of tent caterpillar larvae reared on chokecherry in early spring 2015 was affected by fall webworm presence from the fall of 2014 (the previous growth season). We used first instar larvae from 10 tent caterpillar maternal lines and divided each maternal line into two groups with ~15 larvae in each group. We reared half of the larvae on leaves from chokecherry shrubs without fall webworm or tent caterpillar feeding damage the previous year (hereafter prior fall webworm absence treatment) and half of the larvae on leaves from shrubs that had fall webworm present, but not tent caterpillars present, the previous year (hereafter prior fall webworm presence treatment; $n = 15\text{--}18$ larvae/treatment \times 2 treatments \times 10 maternal lines = 312 total larvae). None of the shrubs had tent caterpillars feeding on them in the field during the experiment. Leaves were collected from multiple shrubs (at least 30 shrubs/treatment), mixed together in collection bags within treatment, and were given to the larvae in a haphazard fashion so that larvae were fed leaves from specific treatments but not from specific shrubs. We reared the tent caterpillar larvae in groups of 15–18 during their first instar and then individually after their mid-second instar in 0.5 L deli containers and gave them fresh leaves from their respective plant treatments as needed (at least twice/week). We did not separate larvae in their first instar because of potential fitness impacts before their second instar due to their gregarious behavior. We measured survival and pupal

mass, which are two proximate measures of fitness for Lepidoptera. Pupal mass has been shown to be a predictor of lifetime fitness for both fall webworms and tent caterpillars, with a positive correlation between pupal mass and the number of eggs laid after eclosion (for a summary table of data from the literature for both species, see Loewy et al., 2013). These measurements allowed us to test the relative quality of each host plant treatment on the performance of tent caterpillar larvae. Survival was measured as the percentage of larvae that survived to pupation for each maternal line in each treatment. We sexed and weighed all pupae 14 days after pupation using a Mettler-Toledo XP6 microbalance (to the nearest 0.01 mg; Mettler-Toledo, Columbus, OH).

We analyzed the results using mixed models with the prior fall webworm presence/absence treatments as the independent variable, larval maternal line as a random independent variable, and pupal mass or larval survival to pupation as the dependent variable. When testing pupal mass, we included sex as a fixed independent variable. Sex was not included in the survival analysis because fall webworm larvae cannot be sexed until after pupation and we were therefore not able to sex the larvae that died before pupation. To calculate the effect size of fall webworm on tent caterpillar pupal mass, we used η^2 which has a range of 0 to 1; the closer the result is to 1, the more of the variance is explained by the variable. We compared any significant ($p < 0.05$) results using Tukey's post hoc analysis.

Do tent caterpillars affect fall webworms through bottom-up effects?

We tested if the fitness of fall webworm larvae reared on chokecherry in fall 2013 was affected by prior tent caterpillar presence in spring 2013 (earlier in the same growing season). We divided fall webworm eggs from 11 maternal lines into two groups that we reared on leaves from two treatments: (1) leaves from shrubs without tent caterpillar or fall webworm feeding damage the previous year (hereafter prior tent caterpillar absence treatment) and (2) leaves from shrubs with prior tent caterpillar presence, but not fall webworm presence, earlier

in the spring (hereafter prior tent caterpillar presence treatment; $n = \sim 17$ larvae/treatment \times 2 treatments \times 11 maternal lines = 366 total larvae). All trees used in the experiments were tagged and monitored for fall webworm and tent caterpillar presence for at least 1 year before we began our experiments. However, not all the trees in the area were monitored, so we do not have broader data on host plant use or population size for either species. We reared fall webworm larvae in an identical manner as the tent caterpillars described above. To measure larval fitness, we recorded survival, larval development time to pupation, and pupal mass and we sexed and weighed pupae 30 days after pupation. Survival was measured as the percentage of larvae that survived to pupation for each maternal line in each treatment. We compared the nutritional quality of the host plants by assessing water content, toughness, hydrogen cyanide, percentage carbon, and percentage nitrogen (Appendix S1).

We analyzed the results using mixed models with the chokecherry treatments (prior tent caterpillar absence and prior tent caterpillar presence) as an independent variable, sex as an independent variable, larval maternal line as a random independent variable, and pupal mass, larval survival to pupation, or development time as the dependent variable. When testing pupal mass, we included sex as a fixed independent variable. Sex was not included in the survival analysis. We compared any significant ($p < 0.05$) results using Tukey's post hoc analysis.

Is competition between fall webworms and tent caterpillars affected by tent caterpillar density?

We manipulated the densities of tent caterpillar larvae on chokecherry shrubs in the field to determine how tent caterpillar density earlier in the season affects fall webworm fitness later in the season in 2015. In the early spring at Betasso Preserve and Boulder Canyon Trail, we manipulated the density of tent caterpillar egg masses on different chokecherry shrubs to create three treatments ($n = 15$ shrubs/treatment): (1) no tent caterpillar egg masses (hereafter prior tent caterpillar absence treatment), (2) one tent caterpillar egg mass (hereafter one tent caterpillar tent treatment), and (3) two tent caterpillar eggs masses (hereafter two tent caterpillar tents treatment). To establish our treatments, we clipped branches with tent caterpillar egg masses from chokecherry shrubs and then used wire to attach these branches to chokecherry shrubs that had no history within the prior year of damage by tent caterpillars. We used the leaves from these manipulated chokecherry treatments to rear fall webworm larvae in the laboratory later in the same growing season ($n = 14$ – 20 larvae/treatment \times 20 maternal lines = 919 total larvae).

We used maternal lines from both our laboratory colony ($n = 18$ maternal lines) and collected from the field in the first instar ($n = 2$ maternal lines). As described for the previous rearing trials, we measured survival and pupal mass as proximate measures of fitness. Survival was measured as the percentage of larvae that survived to pupation for each maternal line in each treatment.

We analyzed the results using mixed models with the tent caterpillar density treatments (one and two tent caterpillar tent and tent caterpillar absence treatments) as an independent variable, maternal line as a random independent variable, and pupal mass, development time, or larval survival to pupation as the dependent variable. When testing pupal mass and development time, we included sex as a fixed independent variable. Sex was not included in the survival analysis because fall webworm larvae cannot be sexed until after pupation and we were therefore unable to sex the larvae that died before pupation. To calculate the effect size of the single tent caterpillar tent treatment on fall webworm pupal mass, we used η^2 . We compared any significant ($p < 0.05$) results using Tukey's post hoc analysis.

Do fall webworms compete with tent caterpillars through top-down effects?

We tested the effect of tent caterpillar presence in the early spring on predation and parasitism of fall webworm larvae later during the same growing season; we conducted this experiment in 2014 at Betasso Preserve and Boulder Canyon Trail. We divided 15 fall webworm egg masses into four groups before they hatched. Egg masses were laid in the laboratory on wax paper and were divided by slicing them into four equal sections using a clean razor blade. This process destroyed the eggs along the edge of the cut but left the other eggs intact. We reared the larvae in the laboratory until their second instar. From each maternal line, we reared two groups on chokecherry with tent caterpillars present early in the season (hereafter prior tent caterpillar presence treatments) and two groups on chokecherry with tent caterpillars absent early in the season (hereafter prior tent caterpillar absence treatments). Once larvae were big enough to deploy in the field (second instar), we placed them on chokecherry shrubs with prior tent caterpillar presence or absence in concordance with their previous rearing history (12–17 larvae/treatment/maternal line). For half of the larval groups in each prior tent caterpillar presence or absence treatment, we placed one group of larvae in green mesh bags (~ 66 cm by 86 cm; 7 holes per cm; Barre Army Navy Store, Barre, VT) to protect them from natural enemies (hereafter unexposed treatment) and left the other group exposed to predators

and parasitoids (hereafter exposed treatment) on the same tree; the mesh bags neither alter larval survival nor noticeably alter their ability to construct a web and only protect larvae from natural enemies (Murphy, 2004). Thus, our experimental design was a complete factorial design crossing prior tent caterpillar presence versus absence with exposure to natural enemies (unexposed vs. exposed; $n = 15$ maternal lines \times 12–17 larvae/treatment \times 4 treatments = 876 larvae total). Our experimental design allowed us to test for possible interactions in bottom-up (variation in foliage quality between the prior tent caterpillar presence/absence treatments) and top-down (predation and parasitism differences between the prior tent caterpillar presence/absence treatments) effects on larval fitness. We attributed the disappearance of larvae in the exposed treatments to death by predation. We collected all larvae from the field in their penultimate instar before they dispersed and continued to rear them in the laboratory until pupation; as described for the previous rearing trials, we measured survival, pupal mass, and larval development time to pupation as proximate measures of fitness. Survival was measured as the percentage of larvae that survived to pupation for each maternal line in each treatment. We also identified all parasitoids that emerged from the larvae and sexed and weighed all surviving pupae 21 days after pupation.

We used mixed models to compare the effects of prior tent caterpillar absence/presence, larval exposure, and the interaction between prior tent caterpillar absence/presence and larval exposure on larval pupal mass, survival to pupation, and development time to pupation. The mixed models included the maternal line as a random effect. In the pupal mass and development time mixed models we also included sex as a fixed effect. We compared the percentage of exposed larvae collected from the field per plant that were parasitized using a mixed model with absence/presence as a fixed independent variable, maternal line as a random variable, and percentage parasitized as the dependent variable. We compared any significant ($p < 0.05$) results using Tukey's post hoc analysis.

RESULTS

Do fall webworms affect tent caterpillars through bottom-up effects?

Fall webworms reduced the pupal mass of tent caterpillars but did not impact survival. Tent caterpillar larvae reared on leaves from the prior fall webworm absence treatment (pupal mass mean = 335.8 ± 23.4 mg) had greater pupal mass than those reared on leaves from the

prior fall webworm presence treatment (pupal mass mean = 278.0 ± 17.1 mg; $F_{1,73} = 6.45$, $p = 0.014$) and female tent caterpillars (pupal mass mean = 388.6 ± 11.4 mg) were significantly heavier than males (pupal mass mean = 181.3 ± 9.1 mg; $F_{1,73} = 214.41$, $p < 0.0001$), but there was no interaction between presence/absence treatments and sex ($F_{1,73} = 2.55$, $p = 0.12$). Tent caterpillar larvae did not differ in their likelihood to survive to pupation when reared on chokecherry from the prior fall webworm absence and presence treatments (fall webworm absence mean = $18.1\% \pm 8.5\%$, fall webworm presence mean = $27.7\% \pm 9.5\%$; $F_{1,9} = 4.45$, $p = 0.064$). The effect size of the fall webworm feeding damage on tent caterpillar pupal mass was $\eta^2 = 0.01$.

Do tent caterpillars affect fall webworms through bottom-up effects?

Prior tent caterpillar presence lowered the fitness of fall webworms by lowering fall webworm pupal mass and increasing development time. We found that larval development time to pupation was 1 day longer on chokecherry with prior tent caterpillar presence (mean = 46.0 ± 0.4 days) compared to larvae reared on leaves from shrubs with prior tent caterpillar absence (mean = 45.1 ± 0.3 days; $F_{1,341} = 4.1$, $p = 0.043$). The pupal mass of fall webworm larvae reared on chokecherry in the prior tent caterpillar presence treatment (mean = 173.8 ± 1.9) was significantly lower than larvae reared on chokecherry from the prior tent caterpillar absence treatment (mean = 178.6 ± 2.1 ; $F_{1,341} = 10.35$, $p = 0.0014$; Figure 2a) and female fall webworms had significantly higher pupal mass (mean = 188.5 ± 1.9) than males (mean = 163.1 ± 1.5 ; $F_{1,341} = 110.1$, $p < 0.0001$). There was no significant interaction between sex and pupal mass ($F_{1,341} = 0.12$, $p = 0.74$). We found no significant difference in survival to pupation (prior tent caterpillar absence mean = $92.9\% \pm 2.9\%$, prior tent caterpillars presence mean = $94.6\% \pm 3.0\%$; $F_{1,21} = 0.15$, $p = 0.71$) among larvae reared on the two host plant treatments. The only significant difference in our host plant quality measures was that spring-damaged leaf treatments had significantly more carbon than undamaged leaves (Appendix S1: Table S1). The effect size of the pupal mass model was $\eta^2 = 0.03$.

Is competition between fall webworms and tent caterpillars affected by tent caterpillar density?

Tent caterpillars caused negative fitness effects (lower pupal mass) on fall webworms via bottom-up effects at

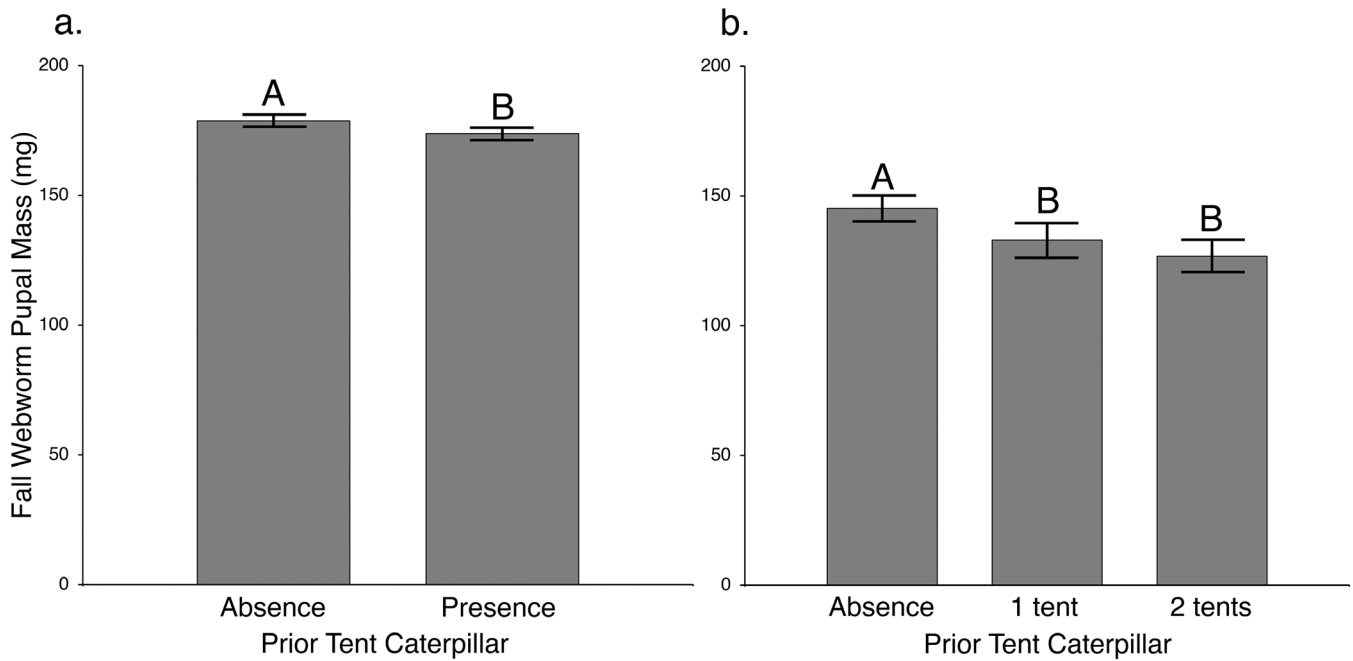


FIGURE 2 (a) Mean pupal mass of fall webworm larvae reared in the laboratory on chokecherry with tent caterpillar absence earlier in the season or tent caterpillar presence earlier in the season. (b) Mean pupal mass of fall webworm larvae reared in the laboratory on chokecherry with tent caterpillars absent earlier in the season (absence), one tent caterpillar tent and associated larvae earlier in the season (1 tent), or two tent caterpillar tents and associated larvae earlier in the season (2 tents). Significant differences between means are indicated with letters and error bars show ± 1 SE.

ambient and high densities but did not impact survival to pupation. Fall webworm larvae reared on host plants with both one and two tent caterpillar tent treatments had significantly lower pupal mass than larvae reared on the prior tent caterpillar absence plants ($F_{2,262} = 3.79$, $p = 0.024$; Figure 2b) and female fall webworms (mean = 134.7 ± 3.3) had greater pupal mass than males (mean = 110.1 ± 2.4 ; $F_{1,262} = 41.24$, $p < 0.0001$) but there was no interaction between pupal sex and tent treatment ($F_{2,262} = 0.55$, $p = 0.58$). Fall webworm larvae did not differ in survival to pupation among the three host plant treatments (prior tent caterpillars absence mean = $26.9\% \pm 5.2\%$, one tent caterpillar tent mean = $22.0\% \pm 4.7\%$, two tent caterpillar tents mean = $29.3\% \pm 4.9\%$; $F_{2,59} = 0.57$, $p = 0.57$). The effect size of the tent caterpillar tent on the fall webworm pupal mass model was $\eta^2 = 0.02$, which is lower than in our previous experiment.

Do fall webworms compete with tent caterpillars through top-down effects?

Fall webworm fitness was negatively impacted by tent caterpillars via top-down effects in terms of survival and pupal mass but not development time. Fall webworm larvae had significantly greater survival to pupation in the

unexposed treatment than in the treatment exposed to predators ($F_{1,55} = 18.78$, $p < 0.0001$), and in the prior tent caterpillar absence treatment than the prior tent caterpillar presence treatment ($F_{1,55} = 5.64$, $p = 0.023$; Figure 3a). We found no interaction between predator exposure and tent caterpillar presence/absence treatments for survival ($F_{1,55} = 0.29$, $p = 0.60$; Figure 3a). For pupal mass, there was a significant interaction between the exposure treatments and the prior tent caterpillar presence/absence treatments with no difference between the unexposed presence/absence treatments but with the larvae in the exposed/absence treatment having greater pupal mass than the exposed/presence treatment ($F_{1,430} = 4.80$, $p = 0.029$; Figure 3b). Unexposed larvae had significantly lower pupal mass than exposed larvae ($F_{1,430} = 178.26$, $p < 0.0001$), but tent caterpillar presence/absence did not significantly impact pupal mass ($F_{1,430} = 2.50$, $p = 0.12$; Figure 3b). There was a significant interaction between the exposure and the presence/absence treatments with the unexposed/presence and exposed/absence treatments having longer development time than the unexposed/absence treatment and no difference between the exposed/presence treatment and the other three treatments ($F_{1,458} = 12.41$, $p = 0.0005$; Figure 3c). Larvae reared on chokecherry in the prior tent caterpillar presence treatments had a significantly longer development time compared with larvae reared on

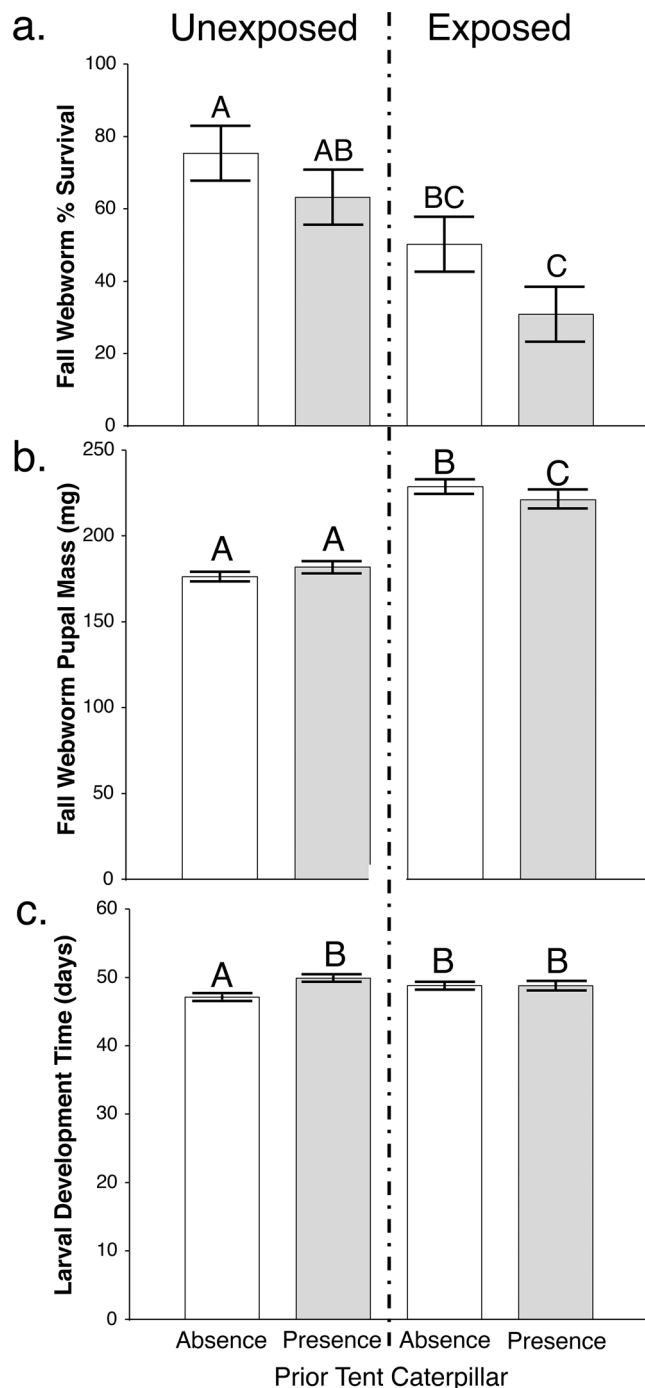


FIGURE 3 Mean percentage survival (a), mean pupal mass (b), and mean development time (c) for fall webworm larvae reared on chokecherry in the field on shrubs with spring tent caterpillar absence or presence and either unexposed or exposed to natural enemies. Significant differences between means are indicated with letters and error bars show ± 1 SE.

chokecherry in the prior tent caterpillar absence treatments ($F_{1,458} = 7.42$, $p = 0.0067$), but no difference between the unexposed and exposed treatments ($F_{1,458} = 0.33$, $p = 0.56$). Percentage parasitism levels per plant of larvae on tent caterpillar tent presence

(mean = $9.2\% \pm 17.1\%$) and absence ($8.7\% \pm 37.4\%$) plants did not differ ($F_{1,25} = 2.73$, $p = 0.14$). Of the 82 parasitoids we collected, 11 (9.7%) were Diptera, 78 (69%) were Hymenoptera, and 24 were unknown larvae.

DISCUSSION

We found evidence that generalist–generalist competition can alter fitness for both species even outside of outbreak conditions. Both fall webworm and tent caterpillar larvae had negative fitness impacts on the other species, confirming that these two generalist species compete indirectly. Due to these negative fitness impacts we might expect both tent caterpillars and fall webworms to avoid chokecherry damaged by the other species of caterpillar. Fall webworms could accomplish this if they are able to recognize the cues left by tent caterpillars, but, because of the timing of their lifecycles (Figure 1, Fitzgerald, 1995; Powell & Opler, 2009), tent caterpillar adult females have no information about which chokecherries will be damaged by fall webworms later in the summer and first instar tent caterpillar larvae are unlikely to move their tent to a new plant (Barnes, personal observation, June, 2014). Thus, not only do tent caterpillars suffer reduced fitness when larvae develop on fall webworm-damaged chokecherry, but tent caterpillar adults and larvae are limited in the ways they can alter their behavior to reduce fitness costs by avoiding chokecherry with fall webworm damage. One way in which tent caterpillars could avoid fall webworm-damaged chokecherry is by using host plant species that are not fed on by fall webworms. Competition-driven host switches have been shown in dietary specialists (Janzen, 1973; Tuda et al., 2014) and temporary switches have been shown in dietary specialist–generalist interactions (Dittrich & Helden, 2020). In situations with high fall webworm densities, selection might drive tent caterpillars to use alternate host plants of equal or near equal nutritional quality that fall webworms do not use. Tent caterpillars at our field site have been recently documented using wax currant, a host plant for tent caterpillars that is not used by fall webworms (Barnes et al., 2016). We have previously shown that wax currant is of comparable quality to chokecherry as a host plant for tent caterpillars and that the use of these two plants is not driven by plant density (Barnes et al., 2016). Further studies will be needed to determine whether the use of wax currant by tent caterpillars at our field sites is driven by competition with fall webworms or some other factor.

Early-season tent caterpillars also had negative effects on late-season fall webworms, via bottom-up forces mediated through the host plant. In our bottom-up

experiments, we found that fall webworm larvae reared on chokecherry with prior tent caterpillar damage (either one or two tents) had lower pupal mass than larvae reared on the plants without tent caterpillars. Thus, fall webworms suffer reduced fitness when feeding on plants with a tent caterpillar density typical in average years, and in outbreak years when shrubs often have at least two tents per plant. We attempted to find the mechanisms underlying fall webworm's and tent caterpillar's impacts on each other, but the only significant result we found—that leaves damaged by fall webworm had significantly more carbon than the undamaged treatments—was extremely small, and we could not rule out a type 1 error. Chokecherry may produce induced defensive responses to a threshold level of herbivory (e.g., Coley & Barone, 1996) or fall webworms may be impacted by chokecherry-induced defenses over a certain threshold regardless of the quantity of damage. Indeed, other studies have found that certain types of damage on other host plants may increase fall webworm fitness (Williams & Myers, 1984), suggesting an additional complexity to this system. In either case, our results suggest that high amounts of leaf damage do not always translate to greater negative fitness impacts on herbivores.

Despite rearing the larvae in an identical fashion and seeing similar trends in our data, the larvae from our summer 2015 experiment had lower pupal mass and survival than the larvae in our summer 2013 experiment. One explanation is that a “100-year” flood in September 2013 that seriously impacted our field sites may have had an effect on the chokecherries that lasted at least 2 years and translated into negative fitness impacts on our 2015 caterpillars. Given the increased frequency of extreme weather conditions due to climate change (IPCC, 2021), these types of impacts could become more common and are worthy of further study. However, although overall chokecherry quality may have decreased over time, our results still point to the negative effects of competition, because our experimental design compares presence/absence treatments within years.

Our results provide evidence for indirect competition between tent caterpillars and fall webworms mediated by both bottom-up and top-down pressures. Our top-down results suggest that predators continue to be attracted to herbivore cues even after larvae have abandoned a host plant. Fall webworms were more likely to survive to pupation when reared on shrubs without tent caterpillar feeding earlier in the season. Our pupal mass results showed that, surprisingly, the caterpillars in our unexposed treatments had lower pupal mass overall than the caterpillars in our exposed treatment, perhaps due to higher intraspecific competition caused by higher larval survival in the unexposed treatments. Fall webworms reared in the

unexposed treatments, which were only impacted by the nutritional quality of the host plant, had the same pupal mass regardless of the presence or absence of tent caterpillar feeding suggesting that, in this experiment, prior tent caterpillar damage did not impact fall webworm fitness through changes in host plant nutritional quality effects on pupal mass. However, the fall webworm reared on the exposed treatments, which were impacted both by the nutritional quality of the host plant and natural enemies, had lower pupal mass when reared on shrubs with prior tent caterpillar damage suggesting that, even in the absence of bottom-up effects, tent caterpillars can impact fall webworm pupal mass through top-down effects.

The negative fitness effects we observed on the tent caterpillar presence/exposed treatment suggest that predators may have continued to use cues from the tent caterpillars, such as tent silk (Waage, 1978) or chemical volatiles (e.g., Turlings et al., 1995), to hunt for prey, which would increase the number of predators in the area. These predators may have had both consumptive and nonconsumptive effects on the fall webworm larvae. Natural enemies can lower prey fitness by their presence alone (Gross, 1993; Thaler & Griffin, 2008). Insects may hide, freeze and stop feeding (Breviglieri & Romero, 2019; Castellanos et al., 2011; Schmitz et al., 1997), or engage in energetically expensive defensive displays (Fitzgerald, 1995) if they detect the presence of a predator. Fall webworms suffer from three types of fitness reduction when competing with tent caterpillars: their food is lower quality, they are more likely to be threatened by predators, and they are more likely to be eaten by predators. Our results support the importance of nonconsumptive predator effects in temporally separated competition. Further investigation into this question is merited to clarify the mechanisms behind and strength of top-down effects in this system.

Our results show an example of generalist insects competing indirectly in a nonagricultural setting. The impact of competition on these species' population dynamics and host plant use remains to be explored. The mechanisms mediating these interactions and their impacts on these insects' populations and the wider community remains unclear. For example, how pathogens that strongly influence caterpillar population cycles (e.g., Myers & Cory, 2016) might impact or be impacted by competition in this system. Further research should be done on interactions between generalist insects, particularly in nonagricultural settings, to determine whether fitness impacts like those we reported are strong enough to affect selection and population cycles.

ACKNOWLEDGMENTS

We thank Boulder County Parks and Open Space and Jefferson County Open Space for research permits and

funding and Sigma Xi and the University of Denver Shubert Award for funding. Robin Tinghitella, Julie Morris, Deane Bowers, the Murphy Laboratory and the University of Denver Ecology and Evolutionary Biologists improved early versions of this manuscript. We thank the editor and two anonymous reviewers for their insightful comments.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Barnes & Murphy, 2022) are available on Figshare at <https://doi.org/10.6084/m9.figshare.19579258.v1>.

ORCID

Elizabeth E. Barnes  <https://orcid.org/0000-0001-7471-9980>

Shannon M. Murphy  <https://orcid.org/0000-0002-5746-6536>

REFERENCES

- Agrawal, A. A. 2000. "Specificity of Induced Resistance in Wild Radish: Causes and Consequences for Two Specialist and Two Generalist Caterpillars." *Oikos* 89(3): 493–500. <https://doi.org/10.1034/j.1600-0706.2000.890308.x>.
- Awmack, C. S., and S. R. Leather. 2002. "Host Plant Quality and Fecundity in Herbivorous Insects." *Annual Review of Entomology* 47(1): 817–44. <https://doi.org/10.1146/annurev.ento.47.091201.145300>.
- Barnes, E. E., S. Gosnell, C. Hallagan, K. Otten, L. Slayter, and S. M. Murphy. 2016. "New Host Plant Record for Western Tent Caterpillar (*Malacosoma californicum*) and its Performance on Two Common Host Plants." *Journal of the Lepidopterists' Society* 70(4): 277–82.
- Barnes, E. E., and S. M. Murphy. 2018. "Time-Lagged Intraspecific Competition in Temporally Separated Cohorts of a Generalist Insect." *Oecologia* 186(3): 711–8. <https://doi.org/10.1007/s00442-018-4067-9>.
- Barnes, E., and S. Murphy. 2022. "Data for Bottom-Up and Top-Down Pressures Mediate Competition between Two Generalist Insects." Figshare. Dataset. <https://doi.org/10.6084/m9.figshare.19579258.v1>.
- Bezemer, T. M., R. Wagenaar, N. M. Van Dam, and F. L. Wackers. 2003. "Interactions between Above-and Belowground Insect Herbivores as Mediated by the Plant Defense System." *Oikos* 101(3): 555–62.
- Bird, G., C. Kaczvinsky, A. E. Wilson, and N. B. Hardy. 2019. "When Do Herbivorous Insects Compete? A Phylogenetic Meta-Analysis." *Ecology Letters* 22: 875–83. <https://doi.org/10.1111/ele.13245>.
- Breviglieri, C. P. B., and G. Q. Romero. 2019. "Acoustic Stimuli from Predators Trigger Behavioural Responses in Aggregate Caterpillars." *Austral Ecology* 44(5): 880–90. <https://doi.org/10.1111/aec.12757>.
- Castellanos, I., P. Barbosa, I. Zuria, T. Tammaru, and M. C. Christman. 2011. "Contact with Caterpillar Hairs Triggers Predator-Specific Defensive Responses." *Behavioral Ecology* 22(5): 1020–5. <https://doi.org/10.1093/beheco/arr085>.
- Coley, P. D., and J. A. Barone. 1996. "Herbivory and Plant Defenses in Tropical Forests." *Annual Review of Ecology and Systematics* 27: 305–35. <https://doi.org/10.1146/annurev.ecolsys.27.1.305>.
- Cooke, B. J., C. J. K. MacQuarrie, and F. Lorenzetti. 2012. "The Dynamics of Forest Tent Caterpillar Outbreaks across East-Central Canada." *Ecography* 35(5): 422–35. <https://doi.org/10.1111/j.1600-0587.2011.07083.x>.
- de Rijk, M., M. Dicke, and E. H. Poelman. 2013. "Foraging Behaviour by Parasitoids in Multiherbivore Communities." *Animal Behaviour* 85(6): 1517–28. <https://doi.org/10.1016/j.anbehav.2013.03.034>.
- Dittrich, A. D. K., and A. J. Helden. 2020. "Can Monophagous Specialists Mediate Host Plant Choices in Generalist Planthoppers (Hemiptera: Delphacidae)?" *Ecological Entomology* 45: 1509–12. <https://doi.org/10.1111/een.12929>.
- Faeth, S. H. 1986. "Indirect Interactions between Temporally Separated Herbivores Mediated by the Host Plant." *Ecology* 67(2): 479–94.
- Fitzgerald, T. D. 1995. *The Tent Caterpillars*. Ithaca: Cornell University Press.
- Gross, P. 1993. "Insect Behavioral and Morphological Defenses against Parasitoids." *Annual Review of Entomology* 38: 251–73.
- Heinrich, B. 1979. "Foraging Strategies of Caterpillars: Leaf Damage and Possible Predator Avoidance Strategies." *Oecologia* 42(3): 325–37.
- Hrbar, H., D. Hattas, and J. T. du Toit. 2009. "Differential Effects of Defoliation by Mopane Caterpillars and Pruning by African Elephants on the Regrowth of Colophospermum Mopane Foliage." *Journal of Tropical Ecology* 25(3): 301–9. <https://doi.org/10.1017/S0266467409005872>.
- IPCC. 2021. *Climate Change 2021: The Physical Science Basis*. Cambridge, UK and New York: Cambridge University Press. https://www.ipcc.ch/report/ar6/wg1/downloads/report/IPCC_AR6_WGI_Full_Report.pdf.
- Janzen, D. H. 1973. "Host Plants as Islands. II. Competition in Evolutionary and Contemporary Time." *The American Naturalist* 107(958): 786–90.
- Jeffries, M. J., and J. H. Lawton. 1984. "Enemy Free Space and the Structure of Ecological Communities." *Biological Journal of the Linnean Society* 23(4): 269–86. <https://doi.org/10.1111/j.1095-8312.1984.tb00145.x>.
- Kaplan, I., and R. F. Denno. 2007. "Interspecific Interactions in Phytophagous Insects Revisited: A Quantitative Assessment of Competition Theory." *Ecology Letters* 10(10): 977–94. <https://doi.org/10.1111/j.1461-0248.2007.01093.x>.
- Karban, R., and I. T. Baldwin. 1997. *Interspecific Interactions: Induced Responses to Herbivory*. Chicago, IL: The University of Chicago Press.
- Klapwijk, M. J., and C. Björkman. 2018. "Mixed Forests to Mitigate Risk of Insect Outbreaks." *Scandinavian Journal of Forest Research* 33(8): 772–80. <https://doi.org/10.1080/02827581.2018.1502805>.
- Loewy, K. J., A. L. Flansburg, K. Grenis, M. K. K. Kjeldgaard, J. McCarty, L. Montesano, J. Vernick, and S. M. Murphy. 2013.

- “Life History Traits and Rearing Techniques for Fall Webworm (*Hyphantria cunea* Drury) in Colorado.” *Journal of the Lepidopterists’ Society* 67(3): 196–205.
- Mäntylä, E., G. A. Alessio, J. D. Blande, J. Heijari, J. K. Holopainen, T. Laaksonen, P. Piirtola, and T. Klemola. 2008. “From Plants to Birds: Higher Avian Predation Rates in Trees Responding to Insect Herbivory.” *PLoS One* 3(7): e2832. <https://doi.org/10.1371/journal.pone.0002832>.
- McCormick, A. C., S. B. Unsicker, and J. Gershenzon. 2012. “The Specificity of Herbivore-Induced Plant Volatiles in Attracting Herbivore Enemies.” *Trends in Plant Science* 17(5): 303–10. <https://doi.org/10.1016/j.tplants.2012.03.012>.
- McGuire, R. J., and M. T. J. Johnson. 2006. “Plant Genotype and Induced Responses Affect Resistance to Herbivores on Evening Primrose (*Oenothera Biennis*).” *Ecological Entomology* 31(1): 20–31. <https://doi.org/10.1111/j.0307-6946.2006.00750.x>.
- Morris, R. J., O. T. Lewis, H. Charles, and J. Godfray. 2005. “Apparent Competition and Insect Community Structure: Towards a Spatial Perspective.” *Annales Zoologici Fennici* 42: 449–62.
- Murphy, S. M. 2004. “Enemy-Free Space Maintains Swallowtail Butterfly Host Shift.” *Proceedings of the National Academy of Sciences of the United States of America* 101(1250): 18048–52. <https://doi.org/10.1073/pnas.0406490102>.
- Myers, J. H., and J. S. Cory. 2016. “Ecology and Evolution of Pathogens in Natural Populations of Lepidoptera.” *Evolutionary Applications* 9(1): 231–47. <https://doi.org/10.1111/eva.12328>.
- Nykänen, H., J. Koricheva, H. Nykanen, J. Koricheva, H. Nykänen, and J. Koricheva. 2004. “Damage-Induced Changes in Woody Plants and their Effects on Insect Herbivore Performance: A Meta-Analysis.” *Oikos* 104(June 2003): 247–68. <https://doi.org/10.1111/j.0030-1299.2004.12768.x>.
- Powell, J. A., and P. A. Opler. 2009. *Moths of Western North America*. Berkeley, CA: University of California Press.
- Rasmann, S., M. De Vos, C. L. Casteel, D. Tian, R. Halitschke, J. Y. Sun, A. A. Agrawal, G. W. Felton, and G. Jander. 2012. “Herbivory in the Previous Generation Primes Plants for Enhanced Insect Resistance.” *Plant Physiology* 158(2): 854–63. <https://doi.org/10.1104/pp.111.187831>.
- Redman, A. M., and J. M. Scriber. 2000. “Competition between the Gypsy Moth, *Lymantria dispar*, and the Northern Tiger Swallowtail, *Papilio canadensis*: Interactions Mediated by Host Plant Chemistry, Pathogens, and Parasitoids.” *Oecologia* 125(October): 218–28. <https://doi.org/10.1007/s004420000444>.
- Sarfraz, R. M., J. S. Cory, and J. H. Myers. 2013. “Life-History Consequences and Disease Resistance of Western Tent Caterpillars in Response to Localised, Herbivore-Induced Changes in Alder Leaf Quality.” *Ecological Entomology* 38(1): 61–7. <https://doi.org/10.1111/j.1365-2311.2012.01404.x>.
- Schmitz, O. J., A. P. Beckerman, and K. M. O. Brien. 1997. “Behaviorally Mediated Trophic Cascades: Effects of Predation Risk on Food Web Interactions.” *Ecology* 78(5): 1388–99. [https://doi.org/10.1890/0012-9658\(1997\)078\[1388:BMTCEO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1388:BMTCEO]2.0.CO;2).
- Shi, P. J., C. Hui, X. Y. Men, Z. H. Zhao, F. Ouyang, F. Ge, X. S. Jin, H. F. Cao, and B. Larry Li. 2014. “Cascade Effects of Crop Species Richness on the Diversity of Pest Insects and their Natural Enemies.” *Science China Life Sciences* 57(7): 718–25. <https://doi.org/10.1007/s11427-014-4681-7>.
- Shiojiri, K., J. Takabayashi, S. Yano, and A. Takafuji. 2002. “Oviposition Preferences of Herbivores are Affected by Tritrophic Interaction Webs.” *Ecology Letters* 5(2): 186–92. <https://doi.org/10.1046/j.1461-0248.2002.00292.x>.
- Stork, W. F. J., A. Weinhold, and I. T. Baldwin. 2011. “Trichomes as Dangerous Lollipops: Do Lizards Also Use Caterpillar Body and Frass Odor to Optimize their Foraging?” *Plant Signaling & Behavior* 6(12): 1893–6. <https://doi.org/10.4161/psb.6.12.18028>.
- Thaler, J. S., and C. A. M. Griffin. 2008. “Relative Importance of Consumptive and Non-Consumptive Effects of Predators on Prey and Plant Damage: The Influence of Herbivore Ontogeny.” *Entomologia Experimentalis et Applicata* 128(1): 34–40. <https://doi.org/10.1111/j.1570-7458.2008.00737.x>.
- Travis, H. J. 2005. “The Effect of Eastern Tent Caterpillar (*Malacasoma americanum*) Infestation on Fall Webworm (*Hyphantria cunea*) Selection of Black Cherry (*Prunus serotina*) as a Host Tree.” *The American Midland Naturalist* 153: 270–5.
- Tuda, M., L. H. Wu, N. Yamada, C. P. Wang, W. J. Wu, S. Buranapanichpan, K. Kagoshima, et al. 2014. “Host Shift Capability of a Specialist Seed Predator of an Invasive Plant: Roles of Competition, Population Genetics and Plant Chemistry.” *Biological Invasions* 16(2): 303–13. <https://doi.org/10.1007/s10530-013-0519-7>.
- Turlings, T. C., J. H. Loughrin, P. J. McCall, U. S. Röse, W. J. Lewis, and J. H. Tumlinson. 1995. “How Caterpillar-Damaged Plants Protect Themselves by Attracting Parasitic Wasps.” *Proceedings of the National Academy of Sciences of the United States of America* 92(10): 4169–74. <https://doi.org/10.1073/pnas.92.10.4169>.
- van Dam, N. M., C. E. Raaijmakers, and W. H. van der Putten. 2005. “Root Herbivory Reduces Growth and Survival of the Shoot Feeding Specialist Pieris Rapae on Brassica Nigra.” *Entomologia Experimentalis et Applicata* 115(1): 161–70. <https://doi.org/10.1111/j.1570-7458.2005.00241.x>.
- Waage, J. K. 1978. “Arrestment Responses of the Parasitoid, *Nemeritis canescens*, to a Contact Chemical Produced by its Host, *Plodia interpunctella*.” *Physiological Entomology* 3: 135–46.
- Wagner, D. L. 2005. *Caterpillars of Eastern North America*. Princeton, NJ: Princeton University Press.
- Wang, X., F. Hua, L. Wang, D. S. Wilcove, and W. Y. Douglas. 2019. “The Biodiversity Benefit of Native Forests and Mixed-Species Plantations over Monoculture Plantations.” *Diversity and Distributions* 25(11): 1721–35. <https://doi.org/10.1111/ddi.12972>.
- Williams, K. S., and J. H. Myers. 1984. “Previous Herbivore Attack of Red Alder May Improve Food Quality for Fall Webworm Larvae.” *Oecologia* 63: 166–70.
- Wink, M. 2010. “Introduction: Biochemistry, Physiology and Ecological Functions of Secondary Metabolites.” *Annual Plant Reviews* 40: 1–19.
- Zakir, A., M. M. Sadek, M. Bengtsson, B. S. Hansson, P. Witzgall, and P. Anderson. 2013. “Herbivore-Induced Plant Volatiles Provide Associational Resistance against an Ovipositing

Herbivore.” *Journal of Ecology* 101(2): 410–7. <https://doi.org/10.1111/1365-2745.12041>.

SUPPORTING INFORMATION

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

How to cite this article: Barnes, Elizabeth E., and Shannon M. Murphy. 2023. “Bottom-Up and Top-Down Pressures Mediate Competition between Two Generalist Insects.” *Ecology* 104(3): e3957. <https://doi.org/10.1002/ecy.3957>