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Competition and Community Interactions of Two Generalist Herbivores

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Abstract

Competition can have far-reaching consequences for the fitness and distribution of many organisms. In herbivorous insects, competition mediated by a third organism is more common than direct competition and has a strong effect on insect communities; yet most research on indirect competition among herbivores focuses on dietary specialists, and those studies that do include generalists tend to rear them on agricultural crops. My project examines species interactions at three levels: intraspecific competition (within species), interspecific competition (between species), and ecosystem engineering effects at the community level. I studied competition and community interactions of two temporally-separated species of herbivorous insects, western tent caterpillars (*Malacosoma californicum*) and fall webworms (*Hyphantria cunea*) on their shared host plant, chokecherries (*Prunus virginiana)*. Within species, I found that time-lagged intraspecific competition reduced larval fitness, that plants that had been fed upon by tent caterpillars the previous season were tougher than plants that had not been fed upon by tent caterpillars, and that there were fewer tent caterpillar egg masses on plants that had tent caterpillars earlier in the season than plants without tent caterpillars. Between species, I found that bottom-up fitness effects on tent caterpillars and both top-down and bottom-up fitness effects on fall webworms which demonstrates that competition can take place in temporally separated generalists through both bottom-up and top-down effects. At the community level, tent caterpillars altered the arthropod community associated with their host plant primarily by increasing predator density by creating structural diversity on their host plants that survives and continued to alter the community into the next year.

My results suggest that dietary generalist insects can have strong competitive and community effects outside of outbreak and agricultural conditions.

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COMPETITION AND COMMUNITY INTERACTIONS OF TWO GENERALIST HERBIVORES

A Dissertation
Presented to
the Faculty of Natural Sciences and Mathematics
University of Denver

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

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by
Elizabeth E. Barnes
November 2017
Advisor: Shannon M. Murphy

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Competition can have far-reaching consequences for the fitness and distribution of many organisms. In herbivorous insects, competition mediated by a third organism is more common than direct competition and has a strong effect on insect communities; yet most research on indirect competition among herbivores focuses on dietary specialists, and those studies that do include generalists tend to rear them on agricultural crops. My project examines species interactions at three levels: intraspecific competition (within species), interspecific competition (between species), and ecosystem engineering effects at the community level. I studied competition and community interactions of two temporally-separated species of herbivorous insects, western tent caterpillars (*Malacosoma californicum*) and fall webworms (*Hyphantria cunea*) on their shared host plant, chokecherries (*Prunus virginiana*). Within species, I found that time-lagged intraspecific competition reduced larval fitness, that plants that had been fed upon by tent caterpillars the previous season were tougher than plants that had not been fed upon by tent caterpillars, and that there were fewer tent caterpillar egg masses on plants that had tent caterpillars earlier in the season than plants without tent caterpillars. Between species, I found that bottom-up fitness effects on tent caterpillars and both top-down and bottom-up fitness effects on fall webworms which demonstrates that competition can take place in temporally separated generalists through both bottom-up and top-down effects.

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CHAPTER 1: TIME-LAGGED INTRASPECIFIC COMPETITION IN TEMPORALLY SEPARATED COHORTS OF A GENERALIST INSECT

Introduction

Competition is a powerful force shaping communities that can alter fitness, species distribution, and population size (Gurevitch et al. 1992, van Veen et al. 2006, Svanbäck and Bolnick 2007, Kaplan and Denno 2007). Despite much compelling evidence regarding the effects of concurrent intraspecific competition on fitness and distribution (Bultman and Faeth 1986, Griffith and Poulson 1993, Awmack and Leather 2002, Svanbäck and Bolnick 2007), few studies investigate the effects of intraspecific competition among temporally separated generations (but see Klomp 1964, Schultz and Baldwin 1982, Kaitaniemi et al. 1999). There is little debate that time-lagged interspecific competition is common (e.g. Schultz and Baldwin 1982, Kaitaniemi et al. 1998, 1999a, Nykanen et al. 2004) and is most often mediated through long-term changes to plant secondary compounds and physiology induced by herbivore damage (Faeth 1986, Awmack and Leather 2002). Given that time-lagged interspecific competition is relatively common and that there is no reason to believe that intraspecific competition should be less common than interspecific competition, we argue that the frequency of occurrence and importance of time-lagged intraspecific competition may be underestimated. For this reason, we tested the impact of time-lagged intraspecific competition on the fitness of a generalist herbivore.

Time-lagged intraspecific competition should be mediated through the same mechanisms as interspecific competition. Interspecific competition in herbivorous insects most commonly takes place indirectly via induced responses in a shared host plant or natural enemies (Kaplan and Denno 2007). When organisms compete indirectly, they do not need to overlap physically or temporally, since their competitive interaction is mediated by another trophic level (Kaplan and Denno 2007). For example, when herbivorous insects feed, they trigger defenses that spread throughout the whole plant (e.g. Faeth 1986, Redman and Scriber 2000, Bezemer et al. 2003, van Dam et al. 2005) and these induced plant defenses affect other insects feeding on that plant (e.g. Faeth 1986, Abdala-Roberts et al. 2012, Uesugi et al. 2016). Since these changes in host plant quality can endure for months or even a year (Kaitaniemi et al. 1998, 1999), the negative effects from herbivore damage may even extend between cohorts of the focal herbivore. In cases of between-season competition, it is impossible for a later cohort to have any impact on a previous cohort and thus this asymmetric interaction might more accurately be termed amensalism (an interaction between two organisms that is negative in one direction and neutral in the other); we use the term competition, however, due to its prevalence in the literature to describe this type of interaction (e.g. Redman and Scriber 2000, Van Zandt and Agrawal 2004, Long et al. 2007, Valdovinos et al. 2013).

If the performance of juvenile insects is negatively affected by a host plant, there may then be evidence of altered oviposition behavior by the adult females in their host plant selection (Thompson 1988). Insects in their adult stage have a range of cues available to them that can provide information about the host plant, not just about the plant species, but a focal plant's history of herbivory and health (Awmack and Leather 2002, Wink 2010). For example, visual and chemical cues indicate the degree to which a plant has been damaged by other herbivores. Insects can detect physical (through touch or vision) and chemical cues (through olfaction or gustation) that provide them with information about the quality of a host plant. For many insects, vision is imperfect at a distance (Schoonhoven et al. 2005, Sponberg et al. 2015), but at close range they can differentiate between plants in terms of their shape (pattern), size (dimensions), and color (spectral quality) (Prokopy and Owens 1983, Renwick 1989, Reeves 2011, McCormick et al. 2012, Nelson and Jackson 2014). Insects that construct elaborate shelters, like tents and webs, leave behind additional evidence of their presence beyond leaf damage cues (Fitzgerald 1995). These visual cues may act as proxies for the degree of activation of host plant defenses and thereby indicate the food quality of the plant (Prokopy and Owens 1983) and although they are not the sole determinant of host plant choice, these cues contribute to oviposition choice in many herbivorous insects (Awmack and Leather 2002). We therefore expect that if larvae compete through their host plant, that adult females will use visual and chemical cues to avoid low quality host plants for their offspring.

We investigated the effect of between-season intraspecific competition on both larval fitness and oviposition choice of a gregarious herbivore: the western tent caterpillar (*Malacosoma californicum*; Packard, Lepidoptera: Lasiocampidae). Tent caterpillars have a single generation per year. They hatch from their egg masses in early spring as larvae, typically construct their tents on their natal host plant, and only venture to other plants to forage if they exhaust their food supply. After pupation in early summer, adults eclose, emerge, and lay their eggs in midsummer (Powell and Opler 2009). Tent caterpillars construct silk tents that last through the summer and, occasionally, into the next year. However, little is known about the cues that adults use to assess oviposition sites beyond the diameter of shrub stems (Schmid et al. 1981, Cadogan and Scharbach 2005, Barnes et al. 2016). We measured the effect of previous-season tent caterpillar presence on tent caterpillar fitness to assess the impact of competition between larval cohorts. We also tested a possible mechanism for these fitness effects by measuring how previous-season tent caterpillar presence affected host plant quality. To test if competition plays a role in oviposition choice, we surveyed host plants for tent caterpillar eggs to determine whether adult tent caterpillar females use signs of early season tent caterpillar presence (e.g. tents, leaf damage) as cues to reject a plant as an oviposition site.

Methods and Materials

Study system

We tested the effects of between-season intraspecific competition with western tent caterpillars (*Malacosoma californicum*) that feed on chokecherry (*Prunus virginiana*). Western tent caterpillars build tents on their host plants and feed gregariously as larvae through their penultimate instar before dispersing. In midsummer, adult females oviposit all of their eggs in a single egg mass on a branch (Fitzgerald 1995). It is unknown if female moths use host plant volatile cues to guide their oviposition choices (Fitzgerald 1995), but they do make oviposition decisions based on branch diameter (Schmid et al. 1981). The eggs overwinter and hatch in the early spring. Although it has not been verified, it is believed that most larvae stay primarily on the host plant that their mother selects (Fitzgerald 1995); it is therefore important that an ovipositing female select a plant that will allow her offspring to thrive. Multiple tent caterpillar colonies may share a single plant, but we only included plants with a single colony in our experiments. Tent caterpillar larvae are generalists when considered across their full geographic range, but frequently specialize at a local level (Powell and Opler 2009). In most areas in the Rocky Mountains, tent caterpillars are found most frequently feeding on quaking aspen, but on the western slope of Colorado they are more commonly found on chokecherry (USFS 2011).

We conducted our study on the eastern slopes of the Rocky Mountains in Colorado, where tent caterpillars feed most frequently on chokecherry and wax currant (*Ribes cereum*) (Barnes et al. 2016). We conducted our field experiments in riparian areas in the foothills of the Colorado Rocky Mountains. We chose study sites in open edge habitats along roads, foot paths and bike paths as tent caterpillars prefer these areas (Fitzgerald 1995, E. Barnes personal observations). We used four field sites in Colorado: Betasso Preserve (N40°1'28", W105°20'19"), Boulder Canyon Trail (N40°0'49", W105°18'35"), Walker Ranch (N39°56'36", W105°20'56), and Centennial Cone Park (N39°45'42.3", W105°20'32.6"). All four sites are near streams in canyons in the foothills of the Rocky Mountains. At each site, chokecherry shrubs grow wild and are dispersed throughout a mix of wooded areas and meadows. We are unable to determine the age of each plant but we only used healthy, mature plants that were capable of producing fruit and at least 80 cm tall in our experiments.

Lab fitness trial

We reared tent caterpillar larvae on chokecherries with and without previous season tent caterpillar presence to test the effect of foliar damage by tent caterpillars on tent caterpillar fitness. We reared larvae in 2015 on leaves collected from chokecherry plants that we tagged and recorded in the previous season in our four field sites (April-June 2014) as either having or not having tent caterpillars present (40 shrubs/treatment). None of these plants had tent caterpillars feeding on them during the rearing trial (2015). In April 2015, we collected first instar larvae from 10 tent caterpillar maternal lines in Boulder Canyon and divided each clutch into two groups of about 15 larvae each. First instar larvae are small, delicate, and often tightly entwined in their tents and are therefore difficult to separate for an exact count without compromising their survival. In the lab in ambient conditions, we reared the larvae in a split clutch design with half of the larvae on leaves from chokecherry with tent caterpillars absent in the previous season (maternal lines n=10, ~15/maternal line, total larvae n=154), and half on leaves from chokecherry with tent caterpillars present in the previous season (maternal lines n=10, ~15/maternal line, total larvae n=159). We collected host plants fresh from the field each day that we fed the experimental larvae in the lab and fed the larvae at least twice per week or as often as needed. Leaves were collected from multiple shrubs 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 recorded two measures of fitness that allowed us to test the relative quality of each host plant treatment on tent caterpillars. First, we measured larval survival to pupation (larvae pupate from late May to mid June), which is a prerequisite to reproduction. Second, we measured pupal mass, which is positively correlated with the number of eggs a female will produce (Loewy et al. 2013). We sexed pupae and measured pupal mass fourteen days after pupation using a Mettler-Toledo XP6 microbalance (to the nearest 0.01 mg; Mettler-Toledo, Columbus, OH).

Host plant quality

We quantified multiple measures of host plant quality including leaf toughness, %water, %N, %C, and cyanogenic glycoside concentration. We collected leaf samples in early June 2016 from chokecherry shrubs with and without larval tent caterpillars the previous season (tent caterpillars present n=26 shrubs; tent caterpillars absent n=30) from Boulder Canyon and Betasso Preserve. We collected the leaves while tent caterpillars were feeding on shrubs nearby, but none of the shrubs had tent caterpillars feeding on them in the growing season that we collected the leaves (2016). We randomly collected a total of 15 leaves from each plant by picking every 5th leaf starting at branch randomly selected using a die. We immediately placed the leaves in a cooler in the field and froze them immediately upon returning to the lab. We kept the leaves flat to ensure that they were not bent or broken.

We measured leaf toughness and %water by randomly selecting 5 leaves per plant that were larger than 3 cm by 2 cm. We thawed the leaves, rinsed them in water to remove dirt, and allowed them to dry for 10 minutes at room temperature (~ 21°C). Next we weighed the leaves as a group (fresh mass) and then measured toughness and the dimensions of each leaf individually. We measured the length of each leaf from the tip of the leaf along the central vein to the base of the stem and measured width across the widest section of the leaf. We measured toughness using a modified version of the sand-pouring method described by Feeny (1970). We attached a safety pin through the leaf 1.5 cm up from the tip of the leaf along the central vein and 0.5 cm from the central vein. The safety pin was attached to a cup by a string. We poured sand into the cup until the safety pin broke all the way through the leaf and weighed the sand. After measuring toughness, we dried all 5 leaves from each plant for 4 days at 60°C and then weighed them once dry. We calculated %water by subtracting dry mass from fresh mass and dividing by fresh mass. For %water and toughness measures on individual leaves, we calculated a mean value per plant and used these means in the analyses. We performed all %water and leaf toughness mass measurements using a Scout Pro Ohaus Balance (Ohaus Corporation, Pine Brook, NJ USA).

Chokecherries are defended by cyanogenic glycosides (Majak et al. 1981). To measure cyanogenic glycoside content and percent carbon (C) and nitrogen (N), we laid out all leaves we collected and counted to the fifth leaf to select three additional leaves that were at least 3 cm by 2 cm in size (these were not the same leaves used to measure toughness and %water). We measured cyanogenic glycoside as hydrogen cyanide (HCN) released from the leaves using the picrate paper method kit containing all materials needed to test HCN (Protocol E, Konzo Prevention Group, Research School of Biology, Australia National University). We cut a section approximately 2 cm by 1 cm out of each of the three leaves, ground them together with a pestle, and measured 100 mg of subsample of the ground leaf material. We quickly poured the leaf material into an airtight tube containing a sheet of linamarase and phosphate buffer paper and covered it with 1 ml of water. We placed a test strip soaked in picrate solution in the container so that it would not touch the leaf material or water, sealed the container and allowed it to sit for 22 hours. We compared the color of the test strip to a color chart to determine the concentration of HCN in the leaves. We placed the remaining leaf material in the drying oven at 60°C for 4 days to obtain leaf material for measuring %C and %N. We combined all three dry leaves and ground them using a Retsch MM 400 Model mixer mill (Retsch GmbH, Haan, Germany), weighed them using a Mettler-Toledo XP6 microbalance (Mettler-Toledo, Columbus, OH), and rolled them into tin capsules (Elementar Americas). We sent the samples to Cornell University Stable Isotope Laboratory to be analyzed for %N and %C using an elemental analyzer-stable isotope ratio mass spectrometer system (Thermo Delta V Advantage IRMS and Carlo Erba NC2500 EA systems).

Survey of tent caterpillar egg masses

We surveyed chokecherry shrubs for tent caterpillar egg masses to assess the oviposition preferences of tent caterpillar adult females. In midsummer 2013 (May-July), we tagged chokecherry shrubs with and without larval tent caterpillars at Boulder Canyon Trail (tent caterpillars present n=19 shrubs; tent caterpillars absent n=22). Shrubs with tent caterpillar damage but no tent caterpillar tents were not included in the survey. In fall 2013, we again surveyed these shrubs for tent caterpillar egg masses after chokecherry shrubs had dropped their leaves and thus it was easier to visually inspect the plants for eggs masses. We surveyed each chokecherry shrub for 5 minutes, carefully inspecting each branch for egg masses and we recorded the presence or absence of tent caterpillar egg masses.

Data analysis

For the lab fitness trial, we determined whether percent larval survival to pupation differed between host plant treatments using an ANOVA with treatment as a fixed effect and maternal line as a random effect. We analyzed pupal mass using an ANOVA with host plant treatment and sex as fixed effects and we tested for an interaction between these fixed effects; we treated maternal line as a random effect. We analyzed chokecherry %water, toughness, %N, %C and hydrogen cyanide (HCN) content using an ANOVA with host plant treatment and collection site as fixed effects. We assessed whether adult tent caterpillars avoid ovipositing on shrubs with early season tent caterpillar presence using a chi-squared test with host plant treatment as the independent variable and the presence of eggs (eggs present vs. eggs absent) as the dependent variable. We used a post-hoc Tukey's HSD test to determine which means were significantly different from one another. All data was analyzed using JMP Pro 10.0.0.

Results

Lab fitness trial

We found a significant interaction between the effects of host plant treatment and sex on tent caterpillar pupal mass ($F_{2,49}$=9.78, p=0.0032; Figure 1); female larvae reared on chokecherry with tent caterpillars absent the previous year had significantly greater pupal mass than those reared on chokecherry with tent caterpillars present the previous year, but there was no difference between treatments for male pupal mass. Female pupae also weighed significantly more than male pupae ($F_{1,49}$=98.8, p<0.0001; male mean=208.0 ± 21.5 mg, female mean=358.6 ± 21.7 mg). Survival did not differ between the larvae reared on chokecherry with tent caterpillars absent the previous year (mean=18.1 ± 8.5%) and those reared on chokecherry with tent caterpillars present the previous year (mean=18.3 ± 7.3%; $F_{1,19}$=0.0005, p=0.98).

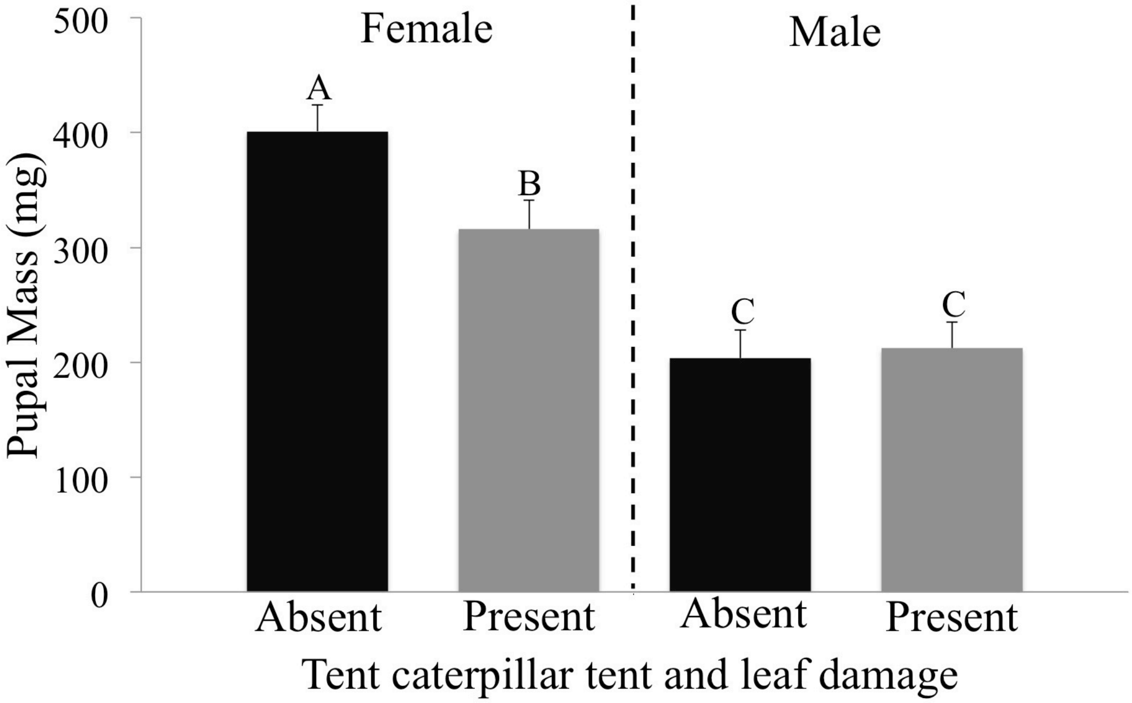


Figure 1. Pupal mass for female and male tent caterpillars reared on chokecherry plants that either did not have previous season tent caterpillar tents or damage (Absent) or that did have previous season tent caterpillar tents and damage (Present). Significant differences between means are indicated with letters and error bars show ±1 SE.

Host plant quality

We found that the toughness of chokecherry leaves was significantly greater on shrubs with tent caterpillars present the previous year than those with tent caterpillars absent the previous year ($F_{1,56}$=5.02, p=0.029) and significantly greater at Betasso Preserve and Boulder Canyon than Centennial Cone Park ($F_{2,56}$=5.92, p=0.0049) but no interaction between them ($F_{2,56}$=0.28, p=0.75; Figure 2). We found that % water was significantly lower at Centennial Cone Park than Boulder Canyon and Betasso preserve ($F_{2,55}$=80.36, p<0.001) and there was an interaction between site and treatment ($F_{2,55}$=3.29, p=0.046), but no difference between tent caterpillar treatments ($F_{1,56}$=0.11, p=0.74; Appendix Table 1). Site ($F_{2,55}$=1.57, p=0.22) and treatment ($F_{1,55}$=3.1, p=0.081) were not different for %N and there was no interaction between site and treatment ($F_{2,55}$=1.62, p=0.21; Appendix Table 1). We found that for %C there was no difference between tent caterpillar treatment ($F_{1,55}$=0.14, p=0.71), site ($F_{2,55}$=1.56, p=0.22; Appendix Table 1), and there was no interaction between the two ($F_{2,55}$=0.49, p=0.62). Hydrogen

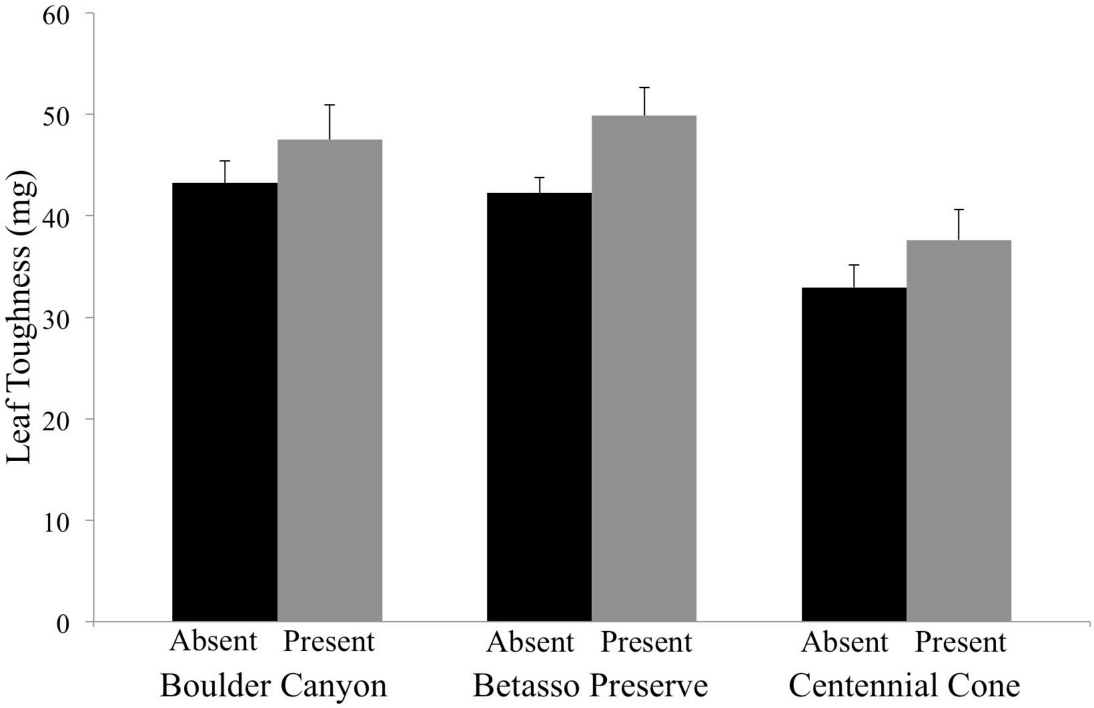


Figure 2. Leaf toughness of chokecherry with no previous season tent caterpillar tents or damage (Absent) or with previous season tent caterpillar tents and damage (Present) at our three field sites. Significant differences between means is indicated with letters and error bars show ±1 SE.

cyanide was lower at Centennial Cone Park than Boulder Canyon and Betasso preserve ($F_{2,55}$=5.77, p=0.0057), but there was no difference between tent caterpillar treatments ($F_{1,56}$=0.43, p=0.51) and no interaction between site and tent caterpillar treatment ($F_{2,55}$=2.64, p=0.081; Appendix Table 1). To ensure that we had a sufficient sample size for our non-significant results, we ran post-hoc power analyses with our means using the recommended statistical power of 0.8 (Cohen 1988). We found that to detect a difference between the means of our samples, we would need 2379 samples for %water, 480 for %N, 1082 for %C, and 4155 for hydrogen cyanide.

Survey of tent caterpillar egg masses

We found that chokecherry shrubs were 6 times more likely to have tent caterpillar egg masses when they had not been previously attacked by tent caterpillars compared to shrubs on which tent caterpillars had been present ($\chi 2$ = 7.73, df = 1, N = 41, P = 0.0054; Figure 3).

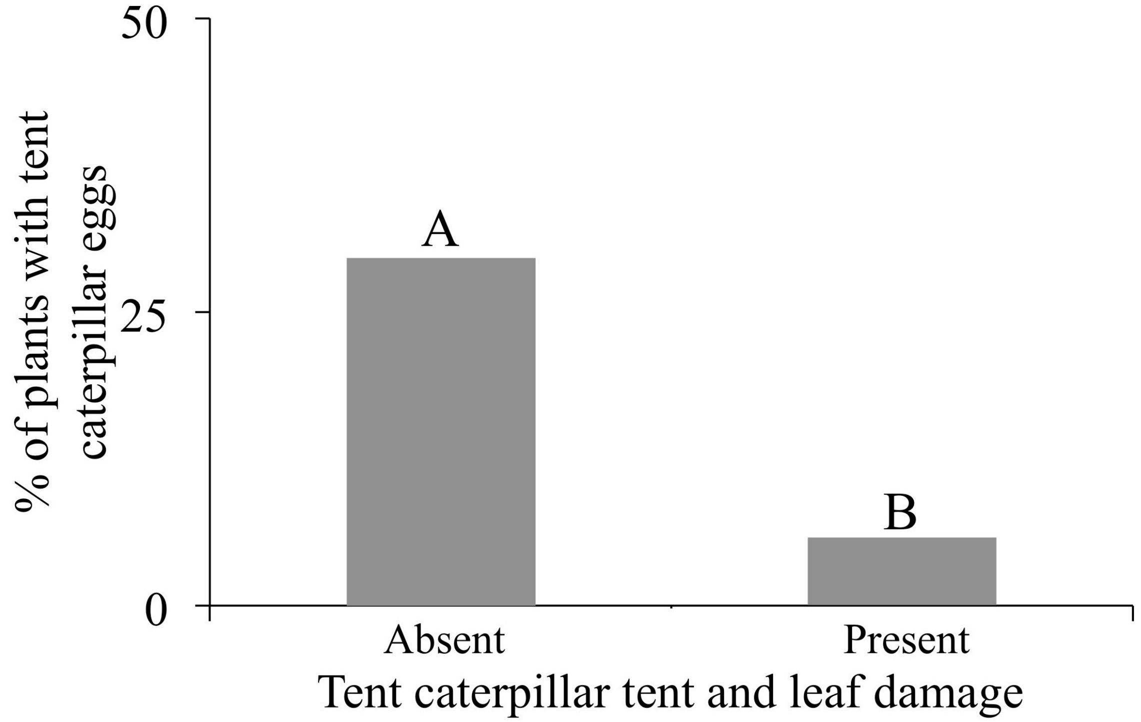


Figure 3. Percentage of chokecherries surveyed with tent caterpillar eggs on plants with no early season tent caterpillar tents or damage (Absent) or with early season tent caterpillar tents and damage (Present). Significant differences between percentages are indicated with letters.

Discussion

The presence of tent caterpillars on a host plant the previous season significantly reduced pupal mass for female tent caterpillars feeding on that plant the next year. Since female pupal mass is positively correlated with the number of eggs that females can lay as adults, females with greater pupal mass have greater lifetime fitness (Loewy et al. 2013). Interestingly, we did not find any negative consequences for male tent caterpillars feeding on previously damaged chokecherry plants as measured by either survival or pupal mass. We note that both of these fitness effects could be caused by inherent differences in host plant quality unconnected to past tent caterpillar feeding. However, in subsequent years all of the plants in our experiment were used by tent caterpillars, which indicates that they all have the potential to be chosen by females as oviposition sites. In addition, if plants with tent caterpillars present the previous year were better host plants, we would have expected the opposite result with our tent caterpillars having higher fitness on those plants than on plants with tent caterpillars absent the previous year. The significant negative effect of host plant damage the previous season on female fitness establishes that host plant mediated competition does occur between cohorts of tent caterpillars through bottom-up effects that negatively affect female larval fitness. We expect this type of interaction to be common in any organism that uses a food resource that is damaged but not killed during feeding, can produce induced defenses, and survives multiple growing seasons.

We found that chokecherry leaves were tougher when tent caterpillars had fed on the plants the previous season. Leaf toughness is an important measure of host plant quality and increased leaf toughness is known to inhibit larval feeding (Gotoh et al. 2011) and has been shown to deter oviposition in some insects (Constant et al. 1996). Leaf toughness is also well established as having a strong effect on the ability of early instars of various tent caterpillar species to bite into their host plant and it has been speculated that toughness plays a key role in larval development (Fitzgerald 1995 and references therein). Our results suggest that increased toughness may cause female tent caterpillar fitness to decrease when they are reared on previously damaged host plants; we did not find any other significant differences in host plant quality between damaged and undamaged plants, but it is unclear why toughness did not similarly affect male larvae. We speculate that since males are smaller than females, they may require less leaf material to pupate and may thus more easily compensate for their slow feeding rate on tougher leaves. If the leaves were tougher because of an induced defense, we expect that the effect would only last through the following growing season, and if the leaves were tougher due to stress on the plant, we expect that the plants might be able to recover within a year of the damage occurring.

Female tent caterpillar adults appear to use cues of prior tent caterpillar feeding damage, such as the presence of tents or leaf secondary compounds, to avoid low-quality host plants for their offspring, as we found fewer tent caterpillar eggs on chokecherry shrubs with tent caterpillar damage and tents earlier in the season compared to shrubs without tent caterpillars earlier in season. Adult female tent caterpillars may choose to avoid ovipositing on host plants with early season tent caterpillar damage by using a combination of visual and chemical cues from tent caterpillar leaf damage and tent caterpillar tents. It is also possible that adult females do not avoid damaged plants, but are instead attacked before they are able to oviposit on damaged shrubs. We have evidence that tent caterpillar tents increase the density of predators on chokecherry, including predators large enough to attack a tent caterpillar moth (Barnes and Murphy in preparation). Whether adult females are attacked while ovipositing near tent caterpillar tents or if their offspring suffer reduced fitness on host plants with prior tent caterpillar damage as we have shown here, both situations would be predicted to select for females that avoid plants that had been previously fed upon by tent caterpillars. Regardless of the mechanism driving avoidance, our oviposition survey demonstrates that time-lagged intraspecific competition alters the behavior of tent caterpillar adults. We speculate that this behavior causes a rough alternation of years of damage on chokecherry with plants having a year of respite after larval feeding. Alternating years of damage and no damage to chokecherries could represent past selection for or future select for longer lasting induced defenses to deter future attack. We expect this pattern to also exist in other systems where the mediating organism both defends itself or suffers a reduction in food quality following an attack and the competing organisms are able to detect cues about food quality.

We show here that there is host plant mediated competition between cohorts of tent caterpillars. Intraspecific competition between temporally separated cohorts of tent caterpillars negatively affects female larval fitness via decreased plant quality and also affects adult oviposition behavior. Time-lagged intraspecific competition is not commonly studied, especially for generalists; our results show that this type of competition can have important fitness consequences and thus our work demonstrates the need for further investigation into the role of between-season intraspecific competition in structuring communities of herbivorous insects.

CHAPTER 2: BOTTOM-UP AND TOP-DOWN PRESSURES MEDIATE COMPETITION BETWEEN TWO GENERALIST INSECTS

Introduction

Competition is one of the fundamental structuring forces in most communities (Gause 1934, Connell 1961, MacArthur and Levins 1967, Svanbäck and Bolnick 2007). In herbivorous insects, indirect competition mediated by a third organism is more common than direct competition (Kaplan and Denno 2007) and has a strong effect on insect communities (e.g. Holt 1977, Wootton 1994, Shiojiri et al. 2002, Van Zandt and Agrawal 2004a); yet most research on indirect competition among herbivores focuses on dietary specialists, and those studies that do include generalists tend to rear them on agricultural crops. Of the papers included in the most recent meta analysis of insect competition (Kaplan and Denno 2007), only 10% of 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%) were tested on agricultural host plants. Thus, only ~5% of studies on indirect competition studied dietary generalists in a non-agricultural setting. Since many dietary generalists insects experience highly destructive outbreaks (i.e. gypsy moths, grasshoppers), we need more studies of these insects in their natural environment and in non-outbreak years to better understand not just competition theory in general but also to better predict their population fluctuations. We therefore conducted multiple experiments testing the indirect competitive effects between two common and widespread generalist herbivores, the fall webworm (*Hyphantria cunea* Drury, Lepidoptera: Erebidae) and tent caterpillars (*Malacosoma californicum* Packard, Lepidoptera: Lasiocampidae).

Competition occurs indirectly by altering bottom-up (e.g. plant secondary compounds, leaf toughness, etc.; e.g. Faeth 1986, Redman and Scriber 2000, Bezemer et al. 2003, van Dam et al. 2005) and/or top down pressures (e.g. predation, parasitism, etc.; e.g. Jeffries and Lawton 1984, Shiojiri et al. 2002, Morris et al. 2005). 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 and 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 others, such as 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 competition in herbivorous insects is often temporally separated (Kaplan and Denno 2007). Thus, insects do not need to be feeding 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 and Johnson 2006, Zakir et al. 2013), severe damage can weaken a plant to the degree that it is no longer able to defend itself (Nykanen et al. 2004). Severe herbivore damage to a host plant can weaken its ability to respond to future damage and reduce the number of defenses with which subsequent herbivores have to contend (Karban and Baldwin 1997). If damage to a host plant is extensive, it may also drop its leaves and reflush. Since young leaves differ from old leaves in terms of chemical defense concentration (Alba et al. 2014) and physical defense density (Matsuki et al. 2004), trees that have reflushed offer herbivores different nutritional quality than trees that have regrown their leaves. Thus, in instances of extensive herbivory (e.g. near complete defoliation of the plant), competing herbivores can have negative or, in some cases, positive fitness effects on their supposed competitors (Harrison and Karban 1986, Van Zandt and Agrawal 2004a, 2004b, Viswanathan et al. 2005, Robert et al. 2012). This high variability in plant response to herbivory means that it is vital to test herbivore responses to different amounts of damage whenever possible when testing competitive effects.

Herbivores may indirectly interact with one another through natural enemies by attracting predators and parasitoids to new foraging areas (e.g. Jeffries and Lawton 1984, Shiojiri et al. 2002, Morris et al. 2005). 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 (Turlings et al. 1995, McCormick et al. 2012, de Rijk et al. 2013). These cues can be generalized or specific to particular types of damages 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-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. Since 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 similar species colonized 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) pressures and top-down (predators and parasitoids). We studied two species of gregarious, dietary generalist Lepidoptera: western tent caterpillar and fall webworm. 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 4). Using this system of two potentially competing, generalist herbivores, 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) Do these caterpillars compete through top-down effects mediated by natural enemies and predators?

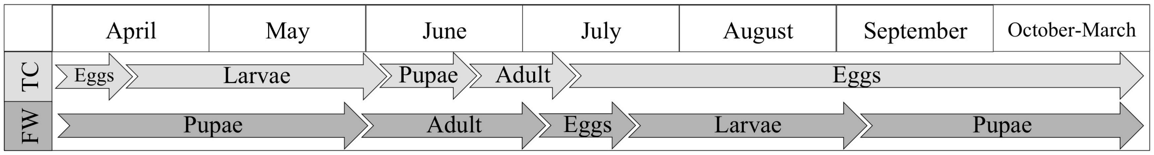


Figure 4. A comparison of a typical life cycle of tent caterpillars (TC; light gray) and fall webworms (FW; dark gray) in the Colorado Rocky Mountains from April to September. Arrows show the time when individuals typically occupy a given stage of the life cycle.

Methods and Materials

Study system

We studied western tent caterpillars and fall webworms in the foothills of the Colorado Rocky Mountains, where they both feed on chokecherry (*Prunus 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 4); the larvae construct dense silk tents that remain on their host-plants through the summer and often into the next year. Tent caterpillars are destructive, but they rarely kill their host-plants (Cooke et al. 2012). Tent caterpillars do not exhibit strong species specific preferences within their most commonly used host plants, 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). 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 4; Powell and Opler 2009). Fall webworms are extreme generalists and can be found feeding on over 400 woody plant species (Wagner 2005), including chokecherry, which is a high quality host-plant where we studied them on the eastern slopes of the Rocky Mountains in Colorado (Loewy et al. 2013). All data was analyzed using JMP Pro 12.0.0.

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). Some evidence suggests that both tent caterpillars and fall webworms may avoid ovipositing on shrubs with tent caterpillar tents and that fall webworm larvae may not survive past their first instar when feeding on plants damaged by tent caterpillar larvae (Williams and Myers 1984, Travis 2005, Barnes and Murphy in preparation). This avoidance behavior by fall webworms suggests that fall webworms and tent caterpillars compete indirectly. We conducted our experiments along paths, roads, and riparian areas in four sites in Colorado: Betasso Preserve (N40°1'28", W105°20'19"), Boulder Canyon Trail (N40°0'49", W105°18'35"), Walker Ranch (N39°56'36", W105°20'56), and Centennial Cone Park (N39°45'42.3", W105°20'32.6"). All four sites are near streams in canyons in the foothills of the Rocky Mountains. We tracked the presence and absence of tent caterpillars and fall webworms at each field sites by numbering them with tags and monitoring them over the growing seasons of 2012-2016.

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

In 2015, we tested if the fitness of tent caterpillar larvae reared on chokecherry in early spring is affected by fall webworm presence from the previous fall (previous growth season). We used first instar larvae from 10 tent caterpillar maternal lines and we divided each maternal line into 2 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 the previous year (hereafter prior fall webworm presence treatment; n=15-18 larvae/treatment x 2 treatments x 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) 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 we did not wish to damage the larvae and they are small, delicate, and often inextricably tangled in their tents before their second instar. We measured survival and pupal mass, which are two proximate measures of fitness for Lepidoptera (Loewy et al. 2013) that allowed us to test the relative quality of each host plant treatment on 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 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. We compared any significant ($P>0.05$) results using a Tukey's post hoc analysis.

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

In 2013, we tested if the fitness of fall webworm larvae reared on chokecherry in the fall is affected by prior tent caterpillar presence in the spring (earlier in the same growing season). We divided fall webworm eggs from 11 maternal lines into 3 groups that we reared on leaves from different treatments: 1) leaves from shrubs without a history of either tent caterpillar or fall webworm feeding damage (hereafter prior tent caterpillar absence treatment), 2) leaves from shrubs with prior tent caterpillar presence earlier in the spring (hereafter prior tent caterpillar presence treatment), and 3) leaves from shrubs that we partially defoliated by hand at the same time as tent caterpillar larvae were present in the field (hereafter prior defoliation treatment; n=~17 larvae/treatment x 3 treatments x 11 maternal lines = 561 total larvae). We included the prior defoliation treatment because some cherry species reflush after damage and these new leaves have different nutritional value and levels of defenses than old leaves (Wink 2010). The prior defoliation treatment provided a way to test whether fall webworm larval responses were due to overall changes in their host-plant caused by tent caterpillars or simply a difference in quality of new leaves compared to old leaves. We reared fall webworm larvae in 0.5 L deli containers and gave them fresh leaves from their respective plant treatments as needed (at least twice/week). Leaves were collected from multiple shrubs (at least 30/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. Larvae were initially reared in groups of 20-30 before being culled to groups of 17 because there are fitness impacts to rearing them individually in the first instar. We then separated larvae into individual deli containers in their late 2nd instar and reared them to pupation. To measure larval fitness, we recorded survival, larval development 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 analyzed the results using mixed models with the chokecherry treatments (prior tent caterpillar absence, prior tent caterpillar presence, and prior defoliation treatments) 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 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. We compared any significant ($P>0.05$) results using a 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 3 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 in the prior year of damage by tent caterpillars. We used the leaves from these manipulated chokecherry treatments to rear fall webworm larvae in the lab later in the same growing season (n=14-20 larvae/treatment x 20 maternal lines = 919 total larvae). We used maternal lines from both our lab 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 development time, survival, and pupal mass as proximate measures of fitness, but did not include the field caught larvae in our development time analysis because we do not know when the field maternal lines hatched. 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 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 a single tent caterpillar tent on fall webworm pupal mass, we used η^2. We compared any significant ($P>0.05$) results using a 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 (Figure 5). Egg masses were laid in the lab 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 lab until their second instar on leaves from each host plant treatments. 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. 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 (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 (Figure 5); the mesh bags do not alter larval survival other than to protect larvae from natural enemies (Murphy 2004). Thus our experimental design was a complete factorial design crossing prior tent caterpillar presence vs. absence with exposure to natural enemies (unexposed vs. exposed; n= 15 maternal lines x 12-17 larvae/treatment x 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 lab 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.

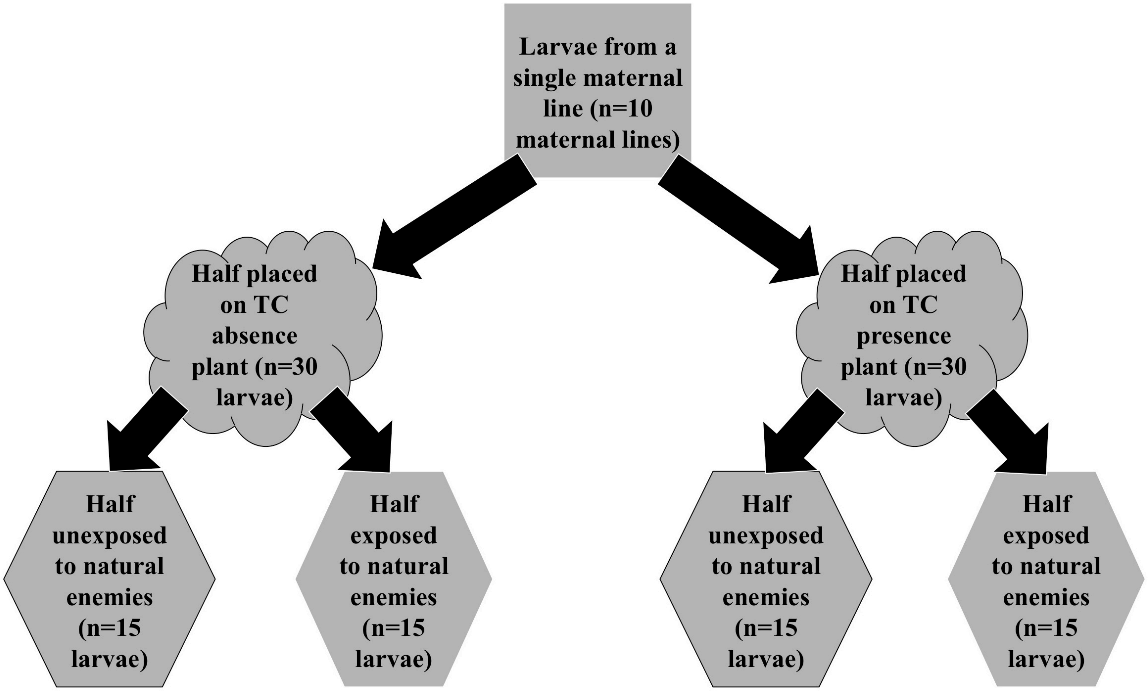


Figure 5. We took fall webworm larvae from a single maternal line (square), divided them into two groups which were reared on shrubs with either tent caterpillars (TC) absence or presence (shrub shapes) in the spring before the experiment took place. We put half of the larvae on each shrub in a mesh bag unexposed to natural enemies (hexagon with black line) and the other half exposed to natural enemies (hexagon without black line).

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 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 percent parasitized as the dependent variable. We compared any significant (P>0.05) results using a Tukey's post hoc analysis.

What plant characteristics mediate competition between tent caterpillars and fall webworms?

To compare the nutritional quality of plant material, we randomly collected chokecherry leaf samples in early June 2016 from shrubs with no prior tent caterpillar or fall webworm presence (N=30) and from shrubs with fall webworm damage from the previous season (N=8). Tent caterpillars feed on their host plants in early June and thus the leaves we collected had the same nutritional value as the leaves tent caterpillars typically eat. Later during the same growing season in mid August 2016, we randomly collected chokecherry leaf samples from shrubs with neither tent caterpillar nor fall webworm damage (N=28), from shrubs with tent caterpillar damage earlier in the season (N=28), and from shrubs with fall webworm larvae presence (N=27). These leaves were collected at a time when fall webworms are typically feeding and thus had the same nutritional value as leaves fall webworms typically eat. For each plant, we collected every 5th leaf starting on a branch selected using a die for a total of 15 leaves per plant. We stored leaves in a cooler with ice packs in the field and then froze them within 8 hours of collection. We kept the leaves flat to ensure that they were not bent or broken to minimize host plant chemistry changes due to damage.

We tested leaf toughness and water content as measures of host plant quality for each sample time and treatment, selecting 5 leaves larger than 3 cm by 2 cm per plant for testing by laying all the leaves collected for each shrub on a table and choosing every fifth leaf. We thawed the leaves, rinsed them in water to remove dirt, and allowed them to dry for 10 minutes at room temperature (~21°C). We measured the length of each leaf from the tip of the leaf along the central vein to the base of the stem and measured width across the widest section of the leaf. Next we weighed the leaves as a group (fresh mass) and then measured toughness for each leaf. We measured toughness using a modified version of the sand pouring method described by Feeny (1970). We attached a safety pin through the leaf 1.5 cm up from the tip of the leaf along the central vein and 0.5 cm from the central vein. The safety pin was attached to a cup by a string. We poured sand into the cup until the safety pin broke all the way through the leaf and weighed the sand. We averaged all five toughness measures and used the single, averaged value in our analyses. After measuring toughness, we dried all 5 leaves from each plant for 4 days at 60°C and then weighed them once dry. We calculated water content by subtracting dry mass from fresh mass and dividing by fresh mass. For both water content and toughness, we averaged the measures for the five leaves into a single measure per plant. We performed all water content and leaf toughness mass measurements to the nearest 0.01 mg using a Scout Pro Ohaus Balance (Ohaus Corporation, Pine Brook, NJ USA).

Chokecherries are chemically defended from herbivores by cyanogenic glycosides (Majak et al. 1981). To measure cyanogenic glycoside content and percent carbon (C) and nitrogen (N), we selected three additional leaves that were at least 3 cm by 2 cm in size from each plant (these leaves were not the same leaves used to measure toughness and water content). By using the same leaves in the cyanogenic glycoside test and the %C and %N tests, we were able to test if there was a relationship between nitrogen in the form of potentially toxic hydrogen cyanide and nitrogen in a nutritionally beneficial form by comparing the cyanogenic glycoside results to the %N results. We measured cyanogenic glycoside as hydrogen cyanide (HCN) released from the leaves using a picrate paper method test kit (Protocol E, Konzo Prevention Group, Research School of Biology, Australian National University). We cut a section approximately 2 cm by 1 cm out of each leaf, ground them together with a pestle, and measured 100 mg of the subsample of the ground leaf material. We quickly poured the leaf material into an airtight tube containing a sheet of linamarase (an enzyme that releases cyanide compounds in plants) paper and phosphate buffer paper and covered it with 1 ml of water. We placed a test strip soaked in picrate solution (a compound that changes color in the presence of cyanide) in the container so that it would not touch the leaf material or water, sealed the container and allowed it to sit for 22 hours. We compared the color of the test strip to a color chart provided in the kit to determine the concentration of HCN in the leaves. We placed the remaining leaf material in the drying oven at 60°C for 4 days for use in testing %C and %N. We combined all three dry leaves and ground them using a Retsch MM 400 Model mixer mill (Retsch GmbH, Haan, Germany), weighed them using a Mettler-Toledo XP6 microbalance (Mettler-Toledo, Columbus, OH), and rolled them into tin capsules (Elementar Americas). We sent the leaf samples to Cornell University Stable Isotope Laboratory to analyze the C and N content using an elemental analyzer-stable isotope ratio mass spectrometer system (Thermo Delta V Advantage IRMS and Carlo Erba NC2500 EA systems).

We analyzed host plant quality using an ANOVA with damage treatment as the dependent variable, collection site as a random variable, and chokecherry water content, toughness, %N, %C, or hydrogen cyanide content as the independent variable. We compared any significant ($P>0.05$) results using a Tukey's post hoc analysis.

Results

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

Female tent caterpillar larvae reared on leaves from the prior fall webworm absence treatment had greater pupal mass than those reared on leaves from the prior fall webworm presence treatment ($F_{1,73}=6.45$, $P=0.014$; Figure 6) and female tent caterpillars were significantly heavier than males ($F_{1,73}=214.41$, $P<0.0001$), but we found no significant difference between the pupal mass of males reared on the prior fall webworm absence (pupal mass mean=335.8±23.4 mg) and presence (pupal mass mean=278.0±17.1 mg) treatments, and there was no interaction between presence/absence treatments and sex ($F_{1,73}=11.39$, $P=0.0031$). 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%±8.5%, fall webworm presence mean=27.7%±9.5%; $F_{1,9}=4.45$, $P=0.064$). The effect size of fall webworm damage on tent caterpillar pupal mass was $\eta^2=0.44$.

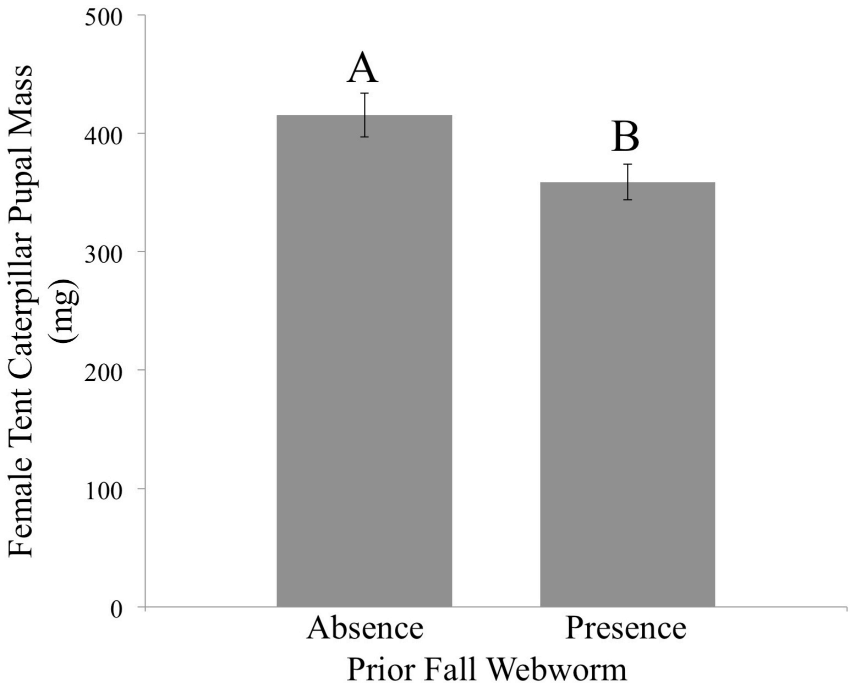


Figure 6. Mean pupal mass of female tent caterpillar larvae reared in the lab on chokecherry with fall webworm larvae either absence or presence the previous season. Significant differences between means are indicated with an letters and error bars show ±1 SE.

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

Fall webworm larvae reared on chokecherry in the prior defoliation treatment had significantly lower pupal mass than larvae reared on chokecherry from the prior tent caterpillar absence treatment ($F_{2,517}$=7.74, P=0.0005; Figure 7) and pupal mass of larvae reared on chokecherry in the prior tent caterpillar presence treatment did not differ from the pupal mass of larvae reared in the other treatments. Female fall webworms (mean=186.8±1.6) had significantly higher pupal mass than males (mean=161.9±1.2; $F_{1,517}$=160.18, P<0.0001) but there was no interaction between sex and presence/absence treatment ($F_{2,517}$=0.02, P=0.97; P>0.05, Tukey's HSD). We found no significant difference in either larval development time to pupation (prior tent caterpillar absence mean=45.1±0.3 days, prior tent caterpillars presence mean=46.0±0.4 days, prior defoliation mean=46.2±0.4 days; $F_{2,516}$=2.72, P=0.067) or survival to pupation (prior tent caterpillar absence mean=92.9±2.9%, prior tent caterpillars presence mean=94.6±3.0%, prior defoliation mean=95.7±1.4%; $F_{2,33}$=0.30, P=0.74) among larvae reared on the three host plant treatments.

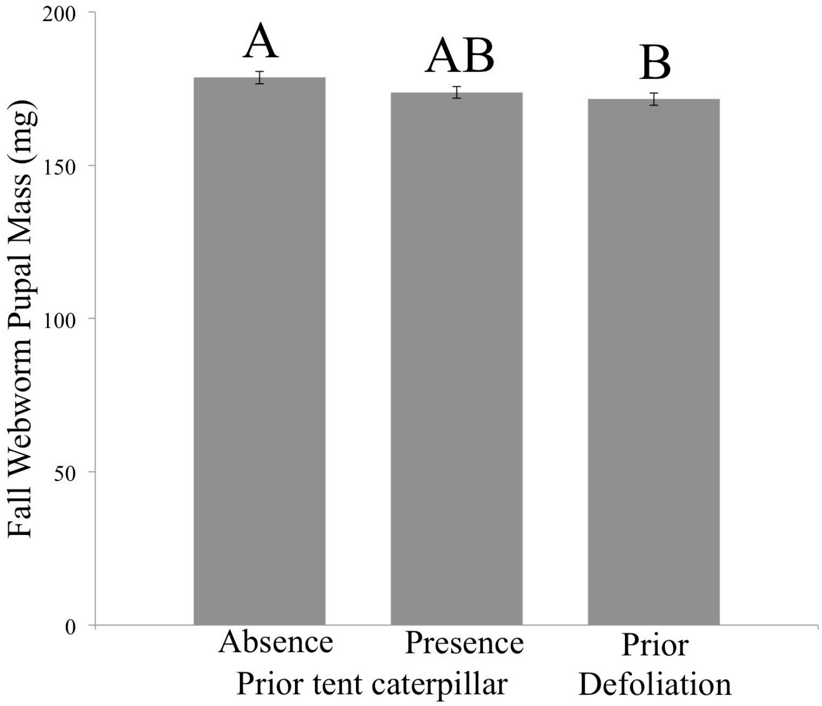


Figure 7. Mean pupal mass of fall webworm larvae reared in the lab on chokecherry with either tent caterpillar larvae absence earlier in the season, tent caterpillars presence earlier in the season, or with a defoliation treatment. The defoliation treatment was included to separate the response of larvae to damaged chokecherry verses a shrub with young, reflushed leaves (but no tent caterpillar damage). Significant differences between means are indicated with letters and error bars show ±1 SE.

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

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 ($F_{2,263}$=3.79, P=0.024; Figure 8) and female fall webworms (mean=134.7±3.3) had greater pupal mass than males (mean=110.1±2.4; $F_{1,263}$=41.24, P<0.001) but there was no interaction between sex and tent treatment ($F_{2,263}$=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±5.2%, one tent caterpillar tent mean=22.0±4.7%, two tent caterpillar tents mean=29.3±4.9%; $F_{2,60}$=0.57, P=0.57). The effect of a single tent caterpillar tent on female fall webworm fitness was η^2=0.22.

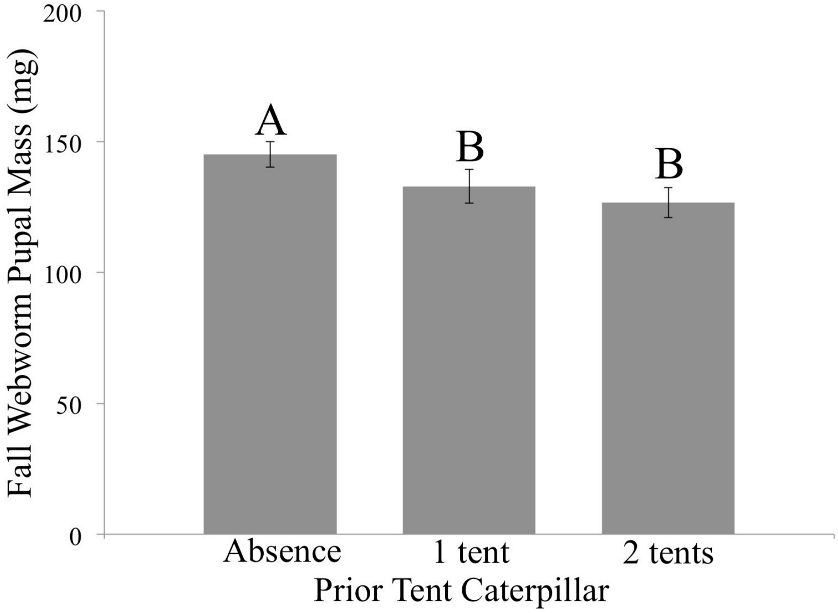


Figure 8. Mean pupal mass of fall webworm larvae reared in the lab on chokecherry with either tent caterpillars absent earlier in the season (absence), one tent caterpillar tent and associated larvae earlier in the season (1 tent), or two tent caterpillar tents and associated larvae earlier in the season (2 tents). Significant differences between means are indicated with letters and error bars show ±1 SE.

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

Fall webworm larvae had significantly greater survival to pupation in the unexposed treatment than in the treatment exposed to predators ($F_{1,56}$=18.78, P<0.0001), and in the prior tent caterpillar absence treatment than the prior tent caterpillar presence treatment ($F_{1,56}$=5.64, P=0.023; Figure 9A). We found no interaction between exposure and presence/absence treatments ($F_{1,56}$=0.29, P=0.60; Figure 9A). 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 ($F_{1,431}$=4.82, P=0.029; Figure 9B). Larvae reared in the unexposed treatments had significantly lower pupal mass than larvae reared in the exposed treatments ($F_{1,431}$=179.46, P<0.001), but there was no difference in larvae reared in the tent caterpillar presence and absence treatments ($F_{1,431}$=2.50, P=0.11; Figure 9B). 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 ($F_{1,459}$=12.73, P=0.0004; Figure 9C). Larvae reared on chokecherry in the prior tent caterpillar presence treatments had a significantly longer development time compared to larvae reared on chokecherry in the prior tent caterpillar absence treatments ($F_{1,459}$=8.32, P=0.0041), but no difference between the unexposed and exposed treatments ($F_{1,459}$=0.43, P=0.51). Larvae on tent caterpillar tent presence (mean=9.2±17.1%) and absence (8.7±37.4%) plants did not differ in the percentage that were parasitized per plant ($F_{1,25}$=2.73, P=0.14). Of the 82 parasitoids we collected, 11 (9.7%) were Diptera, 78 (69%) were Hymenoptera, and 24 were unknown. The majority (95%) of the Hymenoptera parasitoids were Eulophida.

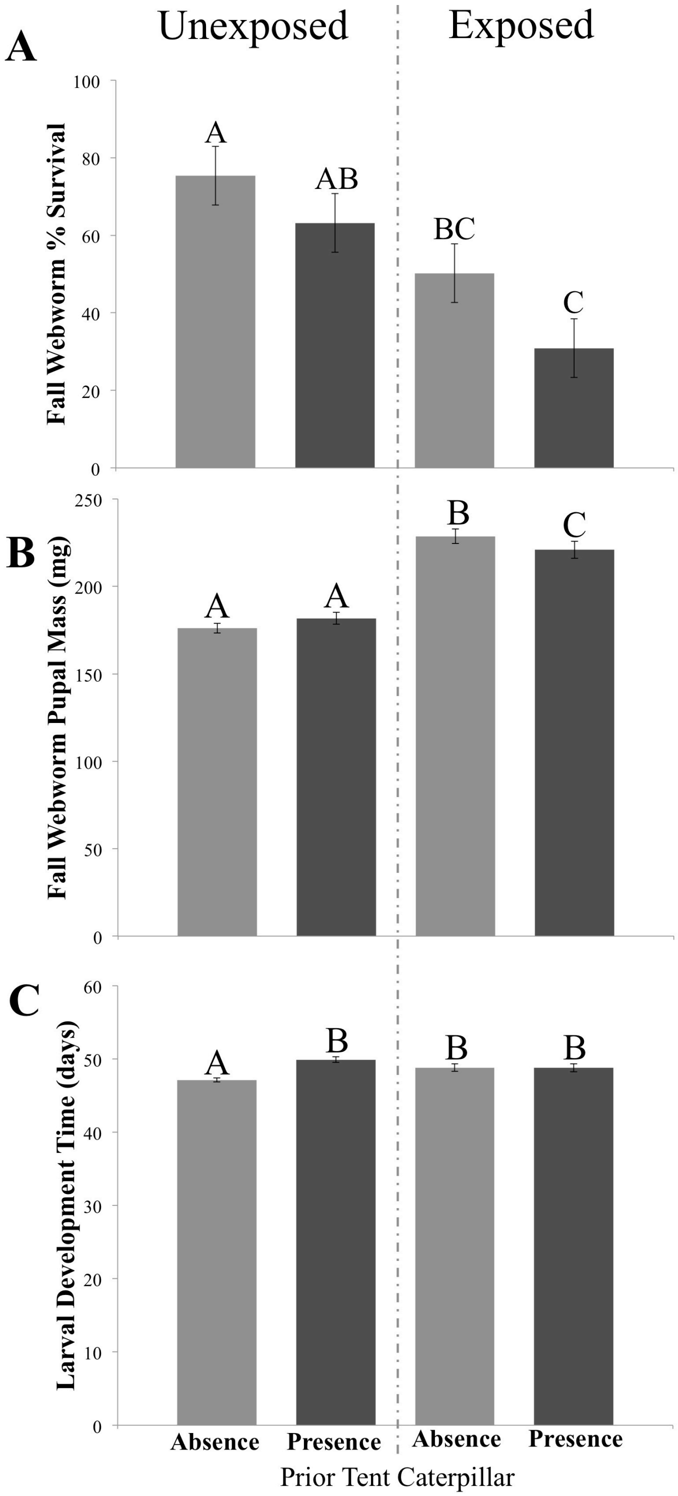


Figure 9. Mean percent survival (A), mean pupal mass (B), and mean development time (C) for fall webworm larvae reared on chokecherry in the field on shrubs with spring tent caterpillar absence or presence and either unexposed or exposed to natural enemies. Significant differences between means are indicated with letters and error bars show ±1 SE.

What plant characteristics mediate competition between tent caterpillars and fall webworms?

For chokecherry leaves collected early season in June, when tent caterpillars were feeding, chokecherry plants that had fall webworms presence the previous season had significantly greater %C than the chokecherry with fall webworms absence ($F_{1,35}$=5.30, P=0.028; Appendix Table 2). For these same plants, we found no significant difference between damaged and undamaged chokecherry for %N ($F_{1,35}$ =0.015, P=0.90; Appendix Table 2), toughness ($F_{1,37}$=0.72, P=0.40; Appendix Table 2), water content ($F_{1,37}$=1.29, P=0.26; Appendix Table 2), or HCN content ($F_{1,36}$=0.86, P=0.36; Appendix Table 2). To ensure that we had a sufficient sample sizes to test our non-significant results, we ran post-hoc power analyses with our means and variances using the recommended statistical power of 0.8 (Cohen 1988). The post-hoc power analysis showed that to detect a difference between the means of our samples, we would need 8,040 samples for %N, 173 for toughness, 169 for water content, and 381 for hydrogen cyanide.

For chokecherry leaves collected later in the season in August, when fall webworms were feeding, both tent caterpillar and fall webworm damaged chokecherry had significantly lower %C than the undamaged chokecherry ($F_{2,87}$=3.14, P=0.049; Appendix Table 2). We found no significant effect of treatment on %N ($F_{2,87}$=0.051, P=0.95; Appendix Table 2), toughness ($F_{2,87}$=1.17, P=0.32; Appendix Table 2), water content ($F_{2,87}$=2.15, P=0.12; Appendix Table 2), or HCN concentration ($F_{2,81}$=0.33, P=0.72; Appendix Table 2). To detect a difference between the means of our samples, we would need 633 samples for %N, 1,378 for toughness, 2,446 for water content, and 1,081 for hydrogen cyanide.

Discussion

We found that both fall webworm and tent caterpillar larvae had negative fitness impacts on one another, confirming that these two generalist species compete indirectly, but that fall webworm has a greater effect on tent caterpillars than tent caterpillars have on fall webworms through bottom-up effects. This finding demonstrates that generalist-generalist competition can alter fitness even outside of outbreak conditions. Tent caterpillar females had lower fitness when reared on chokecherry that fall webworms were present on the previous season, which suggests that fall webworm damage to chokecherry affects the plant quality the following spring. Tent caterpillar adult females have no information about which chokecherries will be damaged by fall webworms (Fitzgerald 1995, Powell and Opler 2009) and first instar tent caterpillar larvae are unlikely to move to a new plant if their original host plants is low quality (Barnes personal observation). Thus, not only do tent caterpillars suffer reduced fitness when larvae develop on fall webworm damaged chokecherry, but neither the adults nor the larvae are able to alter their behavior to reduce fitness costs by avoiding chokecherry with fall webworm damage. Although there are reciprocal effects between the two species, tent caterpillars have more limited paths to reduce fitness impacts than fall webworms. Due to their developmental timing (Fitzgerald 1995, Powell and Opler 2009), fall webworms would simply need to avoid plants with tent caterpillar damage where as tent caterpillars would need to avoid entire species of plants that fall webworms use. We therefore expect that selection would drive tent caterpillars to use alternate host plants that fall webworms do not use and there is some evidence that tent caterpillars may be switching to just such a new host plant, the wax currant (Barnes et al. 2016). Competition driven host switches have been shown in dietary specialists (Janzen 1973, Tuda et al. 2014) but we speculate that a host or host preference shift in a generalist would be limited in alternate host options if the competing animals shared many of the same host plants.

Early-season tent caterpillars also had negative bottom-up effects on late-season fall webworms. In our defoliation experiment, we found that fall webworm larvae reared on the defoliation treatment had lower fitness than larvae reared on the plants without tent caterpillars. Plants frequently respond differently to manual removal of leaves than to herbivory (Lehtilä and Boalt 2008 and references therein), and thus our defoliation treatment may represent a different defensive response closer to high levels of herbivory (i.e. as seen in cases of high tent caterpillar density). We tested this explanation and found that the effect of tent caterpillar density on fall webworm fitness and found that fall webworms had greater fitness on undamaged plants than on either of the treatments with ambient (1 tent) or high (2 tents) tent caterpillar damage. Thus, fall webworms suffer reduced fitness when feeding on plants with tent caterpillar density typical in average years and in outbreak years when shrubs often have two tents per plant. Chokecherry may produce equivalent defensive responses to a threshold level of herbivory (Coley and Barone 1996) or the quantity of defenses may be less important for fall webworm fitness than the presence of any defenses. In either case, our results demonstrate that high amounts of leaf damage do not always translate to higher fitness impacts on herbivores.

In all our feeding trials, we found that both tent caterpillars and fall webworms suffered reduced fitness when feeding on a host plant that the other species had already fed upon, which suggests that their competitive interaction is mediated in part by bottom-up changes in host plant quality. Both our spring and late summer host plant quality results suggest that previous season fall webworm damage, spring tent caterpillar damage, and active fall webworm feeding all produced leaves with significantly more carbon than in undamaged leaves, but there were no differences in our other host plant quality measures. The greater carbon that we observed may be linked to more carbohydrates in damaged chokecherry which have variable effects on different species of insects (Bernays 1998) and, in this case, may lower fitness. Alternatively, chokecherry may produce an induced defense that contains carbon but not nitrogen and this difference may account for the differences in carbon. However, although the differences in carbon between the treatments were significant, they were also extremely small and we cannot rule out a type 1 error. Further testing will be needed to determine if the fitness differences we observed are linked to greater carbon.

Indirect competition between tent caterpillars and fall webworms is mediated by both bottom-up and top-down pressures, strongly suggesting that predators continue to be attracted to herbivore cues even after larvae have abandoned a host plant. Larvae in both unexposed and exposed treatments had lower overall fitness when reared on chokecherry with tent caterpillars present in the spring, which supports our other findings that tent caterpillar damaged chokecherry was of lower nutritional quality than undamaged chokecherry. The negative fitness effects we observed on the tent caterpillar presence/exposed treatment suggest that predators may have continued to use cues left by tent caterpillars, such as tent silk (Waage 1978), to hunt for prey. These predators may have had both consumptive and non-consumptive effects on the fall webworm larvae.

Natural enemies can lower prey fitness by their presence alone (Gross 1993, Thaler and Griffin 2008). Insects may hide, freeze and stop feeding (Schmitz et al. 1997), or engage in energetically expensive defensive displays (Fitzgerald 1995) if they detect the presence of a predator. Our pupal mass and development time results suggest that larvae feeding on plants with prior tent caterpillar presence may have engaged in defensive behaviors that caused them to spend less time feeding than larvae on the tent caterpillar absent treatment because they are more frequently under threat from predators. 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 non-consumptive predator effects in temporally separated competition.

Our results show that generalist insects do compete indirectly. Competition occurs in generalist insects in non-agricultural settings through a combination of top-down and bottom-up forces that have negative fitness impacts on developing larvae. Further research should be done on interactions between generalist insects, particularly in non-agricultural settings so that a more clear understanding of the population dynamics of generalists can be reached. These organisms are often destructive and are important for understanding how arthropod communities interact.

CHAPTER 3: A GENERALIST CATERPILLAR ACTS AS AN ECOSYSTEM ENGINEER BY INCREASING PREDATOR ABUNDANCE WITHIN AND BETWEEN YEARS

Introduction

While all organisms influence their associated communities, some species play a more prominent role than others. Ecosystem engineers are organisms that alter their environment and shape their community by dramatically modifying their habitat and thus influencing associated species (Jones et al. 1994). Ecosystem engineers transform their environment to fit their needs and in doing so create diverse habitat types that have ripple effects through the entire community (Wright and Jones 2006, Hastings et al. 2007). Megafauna (e.g. beavers (Wright et al. 2002), livestock (Derner et al. 2009), and prairie dogs (VanNimwegen et al. 2008)) may be the most visible ecosystem engineers, but organisms that impact microhabitat also have far-reaching impacts on their communities (Folgarait 1998, Jouquet et al. 2006, Marquis and Lill 2010). For example, there is growing evidence that insects that build shelters on plants act as ecosystem engineers (Cornelissen et al. 2016) and that altering even a small section of leaf structure creates a new resource that many other organisms exploit (Lill and Marquis 2003, 2007, Lill et al. 2007, Marquis and Lill 2010). Yet most studies of shelter-building insects only follow the arthropod community for a single growing season and focus on insects that make physically small structures and only damage a small section of their host plant (Cornelissen et al. 2016). In order to fully understand the community wide effects of ecosystem engineers, we need studies that test both how and how long shelter-building arthropods impact their host plant communities. We tested the engineering effects of an insect, the tent caterpillar (*Malacosoma californicum*), that creates long-lasting, large-scale changes to their host plant's structure and chemical profile by the construction of silken tents in which the larvae live. We tested both the mechanism by which they might alter their communities and the longevity of those effects.

Ecosystem engineers can create variations in the host plant architecture that provide a beneficial microclimate that can shelter organisms from environmental conditions (Lill and Marquis 2003) and from predators (Norton et al. 2001). Shelters can protect arthropods from detrimental conditions such as heat or moisture loss (Alonso 1997, Ruf and Fiedler 2002, Fitzgerald et al. 2012). For example, some organisms retreat into plant shelters to regulate their body temperature, thereby not only protecting themselves from extreme temperature fluctuations but also increasing digestion efficiency (Ruf and Fiedler 2002). Structural complexity of plants can also alter the way that predators and parasitoids hunt for prey on and around a plant (Gingras et al. 2002, Gols et al. 2005, Obermaier et al. 2008). Predators are slower at locating prey in more complex environments because they have difficulty navigating, for example between branches (Gols et al. 2005). Structural differences between plants that alter the number of natural enemies attacks have the potential to cause ripple effect through the whole arthropod community. Insects that build shelters on their host plants create structures that, once abandoned, can protect other arthropods from environmental conditions and from attack by natural enemies.

The chemical and visual changes made by ecosystem engineers to their environment can alter the distribution of organisms. Many arthropods make decisions about which area to foraging in by using either the chemical (Renwick 1989, McCormick et al. 2012, Nelson and Jackson 2014) and/or visual (Reeves 2011, Nelson and Jackson 2014) cues associated with the presence of other animals. Cues associated with an herbivore (e.g. host plant volatiles, leaf damage) might be used by another herbivore as information about the health of a host plant (Renwick 1989, Reeves 2011) or by predators as a sign of the presence of a prey item (Weiss 2003, McCormick et al. 2012). Cues associated with predators (e.g. silk webs, chemotactile cues) can cause their prey animals to avoid an area (Buchanan et al. 2017). When arthropods encounter these cues they make decisions about foraging on a particular shrub and thereby alter the community on that plant. If an organism creates particularly long-lasting chemical or visual cues, it has the potential to affect the arthropod community long after it has abandoned a particular location.

Shelter-building arthropods alter their environment in ways that may provide more diverse habitat for other organisms, including predators (Cornelissen et al. 2016). Shelter-building insects can alter food or habitat resources (Cornelissen et al. 2016), which can increase the density of many guilds of organisms, including predators, having ripple effects through the whole arthropod community (Karban 1989, Hodkinson et al. 2001, Schmitz 2003, 2009, Lensing and Wise 2006). For example, increases in spider density can decrease prey numbers and intensify competition with other predators

(Hodkinson et al. 2001). Spiders are found at higher densities in complex habitats, which may have more acceptable web-building locations, higher prey density, or shelter for small or juvenile spiders from intraguild predation (Shear 1986, Finke and Denno 2002, Schmidt et al. 2005, Langellotto and Denno 2006). Since spiders are cannibalistic, they tend not to live in high densities, but highly structured environments can allow for a greater density of spiders by increasing the number of available hiding spaces. Tent caterpillars produce long-lasting chemical and visual prey cues while also building new complex habitat when they construct their tents on their host plants, both of which may attract predators. However, it remains to be tested if predators continue to use abandoned tents, as predators do structures built by other herbivores, such as leaf rollers (Marquis and Lill 2010).

Tent caterpillars are insects that construct elaborate, long-lasting shelters (tents) on their host plants. Unlike many shelter-building herbivores whose shelters fall from their host plant in autumn, tent caterpillar tents are not anchored in leaves, but on branches and therefore often remain on their host plant until the next year. Tent caterpillars construct one or more tents made of silk and frass on their host plants; the tents have a thin outer layer of silk and a dense silk interior (Fitzgerald 1995). The outer layer is frequently damaged or destroyed by midsummer, whereas the inner layer typically lasts the full summer and through the following winter, as it is more sturdy and undergoes a process similar to wool felting (the silk fibers are crossed and tangled to form a cloth-like sheet) when battered by the elements (Barnes personal observation). While the outer layer has loose structure, the inner layer has complex internal passages that are expanded through weathering (Fitzgerald 1995). Tents may have a microclimate that buffer caterpillars against extreme weather fluctuations (Ruf and Fiedler 2002, Fitzgerald et al. 2012) and may heat up while the sun is shining on them (Fitzgerald 1995). Other arthropods may use the tents for their favorable microclimate after the caterpillars have dispersed.

We predicted that tent caterpillar tents would act as ecosystem engineers by having long-lasting impacts on the arthropod food web associated with their host plant by altering the density of predators. The goal of this study was to test the effect that large-scale leaf damage, added host plant structural complexity (tents and damaged leaves), and distinctive visual cues (tents and leaf damage) have on arthropod communities. We suggest that tent caterpillars alter community structure on their host plant by a creating more diverse, architecturally complex habitat. Changes in habitat structure have been repeatedly shown to increase both species richness and diversity (Cornelissen et al. 2016) and we hypothesize that abandoned tents could provide a refuge from predators, hide predators from view of prey, and physically shelter arthropods from adverse weather (e.g. from wind or rain). We had three research objectives. First, we tested if tent caterpillars act as ecosystem engineers and thus change the arthropod community and, second, tested the longevity of those effects. Third, if tent caterpillars are ecosystem engineers, we tested which cues or changes to their host plant are primarily responsible for altering the arthropod community.

Materials and Methods

Study system

We conducted our experiments in riparian areas in the foothills of the Colorado Rocky Mountains at five field sites: Betasso Preserve (N40°1'28", W105°20'19"), Boulder Canyon Trail (N40°0'49", W105°18'35"), Walker Ranch (N39°56'36", W105°20'56), Centennial Cone Park (N39°45'42", W105°20'32"), and Mount Galbraith Park (39°46'18"N 105°15'08"W). All five sites are near streams in canyons at the base of the Rocky Mountains. Tent caterpillars are gregarious caterpillars that live in colonies of up to 100 individuals; larvae hatch from eggs in early spring as the buds of their host plants are opening, feed on their host plant through early summer, and disperse from their tents in early summer. Thus, tent caterpillars alter their host-plants from the start of the growing season but, as there is only a single generation per year in the Rocky Mountains, they are only present on the plant from early spring to the beginning of summer. Tent caterpillar larvae work collectively to construct tents on their host-plants and will often completely defoliate the branch where their tent is located (Fitzgerald 1995). While tent caterpillars are generalists, they frequently feed on chokecherry (*Prunus virginiana*) at our field sites (Barnes et al. 2016), which was the focal host plant for our study.

Do tent caterpillars alter arthropod communities on their host plants?

To test the impact of tent caterpillars on arthropod communities, we compared arthropod communities on chokecherries with abandoned tent caterpillar tents and tent caterpillar damage absent or present (hereafter referred to as tent caterpillar tents). We collected samples at two time points in 2014, midsummer in July (present n=34, absent n=31) and late summer in August (present n=50, absent n=40; Appendix Table 3). We chose the time points to test if there was a difference in the impact of tent caterpillars on arthropods shortly after the tents have been abandoned (July) vs. at the end of the summer (August). We randomly selected branches from upper, mid, lower, and tent sections of each chokecherry shrub (Figure 10). For the shrubs that did not have a tent caterpillar tent, we used a branch of the shrub that was similar to the location of the tent on the plant with a tent caterpillar present in the spring. The four branch locations ensured that we collected a representative sampling of the community of arthropods on the entire host plant as there can be differences in the types of organisms found at different locations on plants. We searched each branch for arthropods for 5 minutes and collected any arthropods we found during that time for later identification. In the August survey, we collected all tents in sealed plastic bags, stored them in a cooler with ice packs in the field, and froze them within 8 hours of being collected. We did not collect the tents in the July survey because we intended to compare the arthropod communities on the same shrubs in July and August. However, some shrubs included in the July survey were cut down by trail maintenance crews and were replaced with nearby shrubs for the August survey. We were therefore unable to make a direct comparison between the arthropod community of the shrubs in July and August.

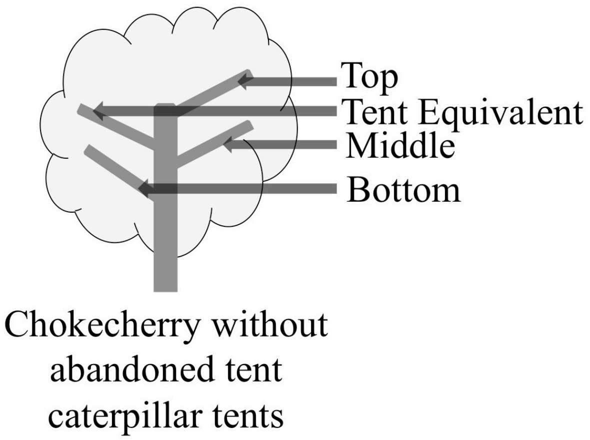


Figure 10. Locations of branches that were used for collection of arthropods in a survey of chokecherry shrubs either with (present) or without (absent) an abandoned tent caterpillar tent.

We removed all arthropods from the tents and identified any that could be seen with the naked eye. Organisms collected in the field on leaves and branches were visually easier to distinguish from the background than organisms in the tents, which were surrounded by small particles of frass and leaves. However, using a microscope we were able to see many organisms in the tents that may have been present in the field but were not visible to the naked eye and were not collected. Therefore, in order to ensure that our arthropod counts on the tent equivalent branch and the tent branch were comparable, we used a microscope to sort through the tents and remove arthropods but only included in our count those organisms that could be seen with the naked eye once separated from the tent. We identified all arthropods to order, and to lower classifications when possible and classified the arthropods as predator (any arthropod that was a natural enemy of other arthropods, including ants, wasps, spiders, etc.), herbivore (any arthropod that feeds on living plant material, including caterpillars, sawfly larvae, plant hoppers, etc.), or unknown (any arthropod that we could not categorize without further identification). We did not include any eggs, exoskeletons, pupal cases, or other evidence of previous occupation of the tent in our analysis as we could not be sure that these arthropods used the shrub after it was abandoned by the tent caterpillars. It should be noted that tents do contain many additional predacious and detritivorous arthropods (i.e. mites) that we did not count.

To test if there was an effect of abandoned tent caterpillar tents on the presence of any arthropods, we used a chi-squared test with presence or absence of arthropods as our dependent variable and abandoned tent caterpillar tent present/absent as our independent variable. We compared arthropod abundance with a two way ANOVA with total arthropod abundance, spider abundance, predator abundance, or herbivore abundance as a dependent variable, field site as a dependent variable, and abandoned tent caterpillar tent present/absent as our independent variable. We tested the July and August surveys separately because the survey methodology was not identical at each time point (tents were collected in August but not July). In the August survey, we compared the abundance of arthropods in the tents to the abundance of on the tent equivalent branch using a Wilcoxon test. We used the Wilcoxon test because our results were zero inflated. We compared any significant ($P>0.05$) results using a Tukey's post hoc analysis.

Do tent caterpillars have long-term impacts on arthropod communities?

In order to determine if the influence of tent caterpillars on arthropod communities extends for longer periods of time, we collected tent caterpillar tents in Boulder Canyon Trail one year after they were built (April 2017). Old tents are often damaged by weathering and are decoupled from tent caterpillar leaf damage cues because chokecherries drop all of their leaves, including damaged leaves, the previous autumn. Thus, the only remaining effects from the tent caterpillars on the chokecherries are from tents and any induced defenses that extend into the subsequent growing seasons. We surveyed chokecherry plants with an abandoned tent caterpillar tent from the previous year (n=20) and plants that did not have an abandoned tent caterpillar tent the previous year (n=20). We searched one branch with a tent caterpillar tent from the previous year or an equivalent branch on a shrub without tent caterpillars the previous year for 30 seconds each. We collected all tents in sealed plastic bags, stored them in a cooler with ice packs in the field, and froze them within 8 hours of being collected. We removed arthropods from the tents and identified them in the same manner as described in the previous community survey.

To test if there was an effect of abandoned tent caterpillar tents on the presence of any arthropods, we used a chi-squared test with presence or absence of arthropods as our dependent variable and abandoned tent caterpillar tent present/absent as our independent variable. We tested the effect of abandoned tent caterpillar tents on the presence of predators and herbivores using a Wilcoxon test where predator or herbivore abundance was our dependent variable and tent present/absent was our independent variable. We compared the chokecherry with an abandoned tent caterpillar tent present the previous year to shrubs with a tent caterpillar tent absent using a Wilcoxon test where total arthropod abundance or spider abundance was our dependent variable and tent caterpillar tent present/absent was our independent variable. We used the Wilcoxon test for predators, herbivores, and tents vs. tent equivalent branches because our results were zero inflated.

How do tent caterpillars alter their host plant's arthropod community?

In July 2016, we conducted a manipulative experiment to determine the mechanism through which tent caterpillars alter their host plant's arthropod communities by separating the chemical, visual, and structural cues from tents and leaf damage. We created 6 chokecherry treatments to manipulate chemical and visual cues from the tents and leaf damage with one of each treatment in a patch of chokecherries: 1) chokecherries with no tent caterpillar damage and no tent treatment (no chemical, visual, or structural cues from tent or herbivore damage; hereafter unchanged undamaged treatment, 2) chokecherries with no tent caterpillar damage that we covered in broken-apart tent caterpillar tents (chemical cue of the tent, but no visual cue or herbivore damage; hereafter broken tent treatment), 3) chokecherries with no tent caterpillar damage with false wool tents attached (visual and structural cues from tent, but no chemical cues from tent or cues from herbivore damage; hereafter false tent treatment), 4) chokecherries with no tent caterpillar damage to which we attached whole tent caterpillar tents (visual and chemical cue of the tent, but no herbivore damage; hereafter attached tent treatment), 5) chokecherries with tent caterpillar damage and their tents removed (herbivore damage visual and chemical cues, but no tent cues; hereafter tent removed treatment), and 6) chokecherries with both tent caterpillar damage and tents (visual and chemical cues from tent and herbivore damage; hereafter unchanged tent treatment; Figure 11). We constructed the false tents to closely mimic the internal and external structure of tent caterpillar tents using dead branched twigs and wool. We needle-felted the wool (a process that compacts the wool and tangles the fibers) so that it more closely mimicked the structure of tent caterpillar tents and to ensure that it would not break apart during the experiment. We wrapped the wool around the twigs using the smaller branches on the twigs as anchor points. We left a cavity inside the false tents, included layers of wool, and left two small holes in the wool so that they were similar to the structure of tent caterpillar tents. We performed manipulations in mid-July at Betasso Preserve (n=5 shrubs/treatment), Boulder Canyon Trail (n=11 shrubs/treatment), Walker Ranch (n=5 shrubs/treatment), and Mount Galbraith Park (n=9 shrubs/treatment; total of n=30 shrubs/treatment for 180 shrubs total) after all tent caterpillars had abandoned their tents and conducted our community survey and collected the tents and arthropods in August. We searched all branches and stems on each chokecherry for arthropods for 10 minutes and collected any arthropods we found during that time. We collected all tents in sealed plastic bags, stored them in a cooler with ice packs in the field, and froze them within 8 hours of being collected. We identified the arthropods in the manner described in previous surveys.

To test if there was an effect of the manipulated cues on the presence of any arthropods, we used a chi-squared test with presence or absence of arthropods as our dependent variable and the cue manipulation treatments as our independent variable. We compared arthropod abundance with a mixed-model with total arthropod abundance or spider abundance as our dependent variable, and cue manipulation treatment as our independent variable. We included site and patch as random variables. We compared any significant ($P>0.05$) results using a Tukey's post hoc analysis.

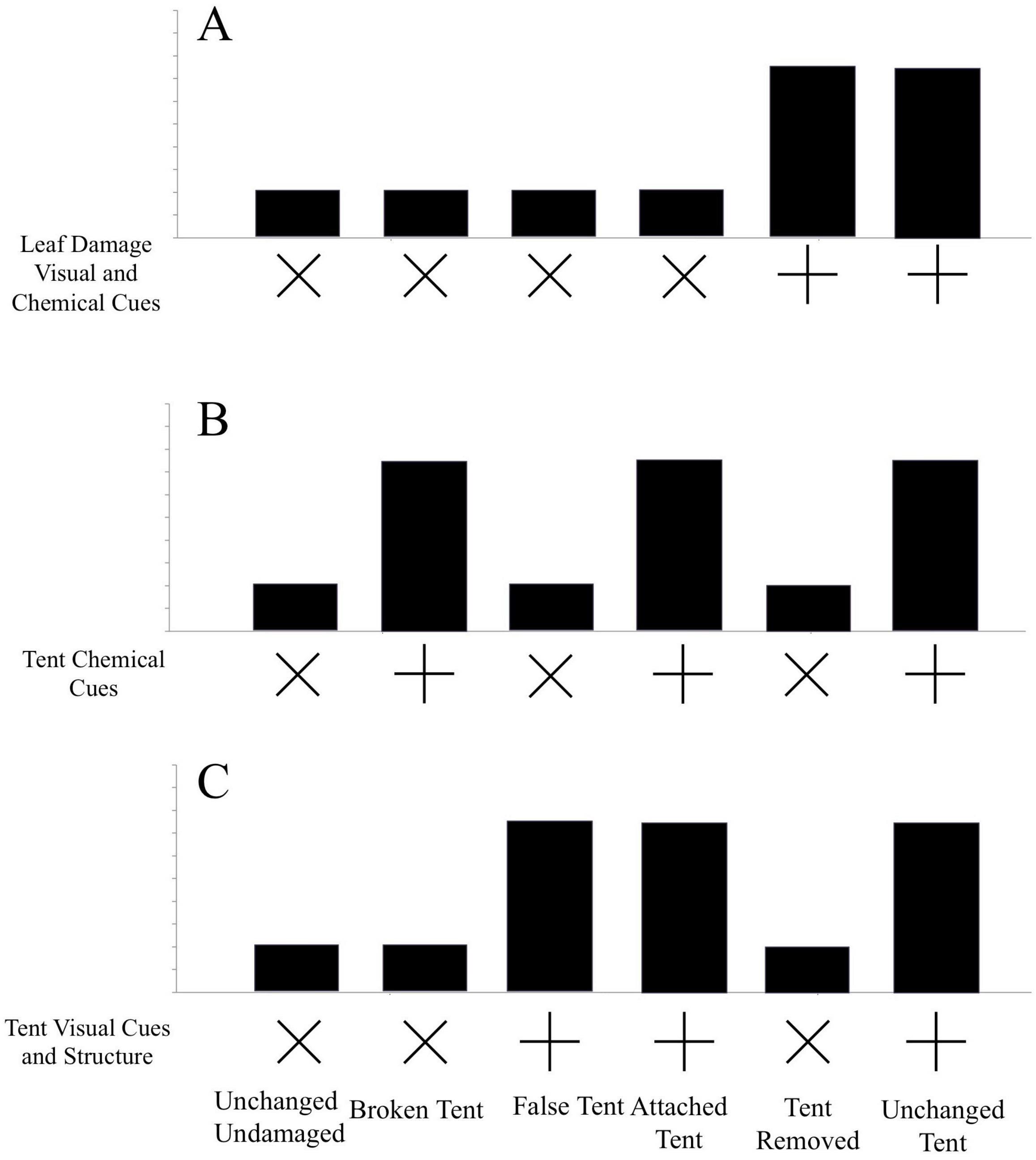


Figure 11. Predictions for arthropod community response when leaf damage visual and chemical cues (A), tent chemical cues (B), or tent visual cues and tent structure (C) are the mechanism affecting arthropod community abundance. Plus marks (+) indicate that a cue is present in a treatment and x marks (X) indicate that the cue is absent in a treatment. We expect that if one of the three cues is the mechanism driving higher arthropod abundance on shrubs with abandoned tent caterpillar tents that treatments with those cues should have higher abundance than the other treatments. For example, if tent chemical cues are driving arthropod abundance, the broken tent, attached tent, and unchanged tent treatments should have higher arthropod abundance than the other three treatments.

Results

Do tent caterpillars alter arthropod communities on their host plants?

In the July survey, the shrubs that an abandoned tent caterpillar tent present (total arthropods=25) or absent (total arthropods=21) on them were equally likely to have arthropods on them (χ^2=0.062, df=1, N=65, p=0.80). Plants in Centennial Cone Park (mean=4.4±0.6) had significantly more arthropods than the other three sites (Betasso mean=0.9±0.7, Boulder mean=1.8±0.5, Walker Ranch mean=0.4±0.9; $F_{3,65}$ =7.47, p=0.0003), but there was no effect from the presence (mean=2.4±0.5) or absence of tent caterpillars (mean=1.9±0.5; $F_{1,65}$ =0.44, p=0.51) or an interaction between site and tent caterpillar present/absent treatment ($F_{3,65}$ =0.35, p=0.79). Spiders did not differ in abundance between chokecherry with tents present (mean=0.3±0.1) or absent (mean=0.2±0.1; $F_{1,65}$ =0.0010, p=0.97), location (Betasso mean=0±0.2, Boulder mean=0.5±0.1, Centennial Cone mean=0.2±0.1, Walker Ranch mean=0±0.2; $F_{3,65}$ =2.72, p=0.05), and there was no interactions between tent present/absent plants and location ($F_{3,65}$ =2.11, p=0.10). There was no difference in abundance of predators between chokecherry with tents present (mean rank=34.50) or absent (mean rank=31.35; Z=-0.86, N=90, p=0.39) and no difference in the abundance of herbivores between plants with tents present (mean rank=32.61) or absent (mean rank=33.41; Z=0.17, N=90, p=0.86).

In the August survey, significantly more chokecherry plants that had an tent caterpillars ten present had arthropods present (36 plants) than shrubs with an tent caterpillar tent absent (17 plants; χ^2=7.98, df=1, N=90, p=0.0047). Chokecherry with tent caterpillar tents present had significantly more arthropods than the tent caterpillar absent chokecherry (Figure 12; $F_{1,90}$ =15.31, p=0.0002), but there was no effect from the site (Betasso mean=1.8±0.4, Boulder mean=1.4±0.3, Centennial Cone mean=1.8±0.3, Walker Ranch mean=0.8±0.5; $F_{3,90}$ =0.80, p=0.50) and no interaction between the site and the tent caterpillar present/absent treatment ($F_{3,90}$ =0.88, p=0.45). Spiders had a greater abundance on tent caterpillar present than tent caterpillar absent chokecherry (Figure 12; $F_{1,90}$ =7.85, p=0.0063), and had neither a difference in abundance between sites (Betasso mean=0.6±0.2, Boulder mean=0.7±0.2, Centennial Cone mean=0.7±0.2, Walker Ranch mean=0±0.3; $F_{3,90}$ =1.28, p=0.29) nor an interaction between site and tent caterpillar present/absent treatments ($F_{3,90}$ =0.63, p=0.60). Predators were more abundant on chokecherry with tent caterpillar tents present (mean rank=55.71) than on plants with tents absent (mean rank=32.74; Z=-4.47, N=90, p<0.0001), but herbivores did not differ in abundance between chokecherry with tents present (mean rank=47.12) and tents absent (mean rank=43.48; Z=-1.15, N=90, p=0.25). The tents (mean rank=58.39) had a greater abundance of arthropods than the tent equivalent branches on chokecherry that had tent caterpillars absent (mean rank=29.38; Z=-5.87, N=90, p<0.001).

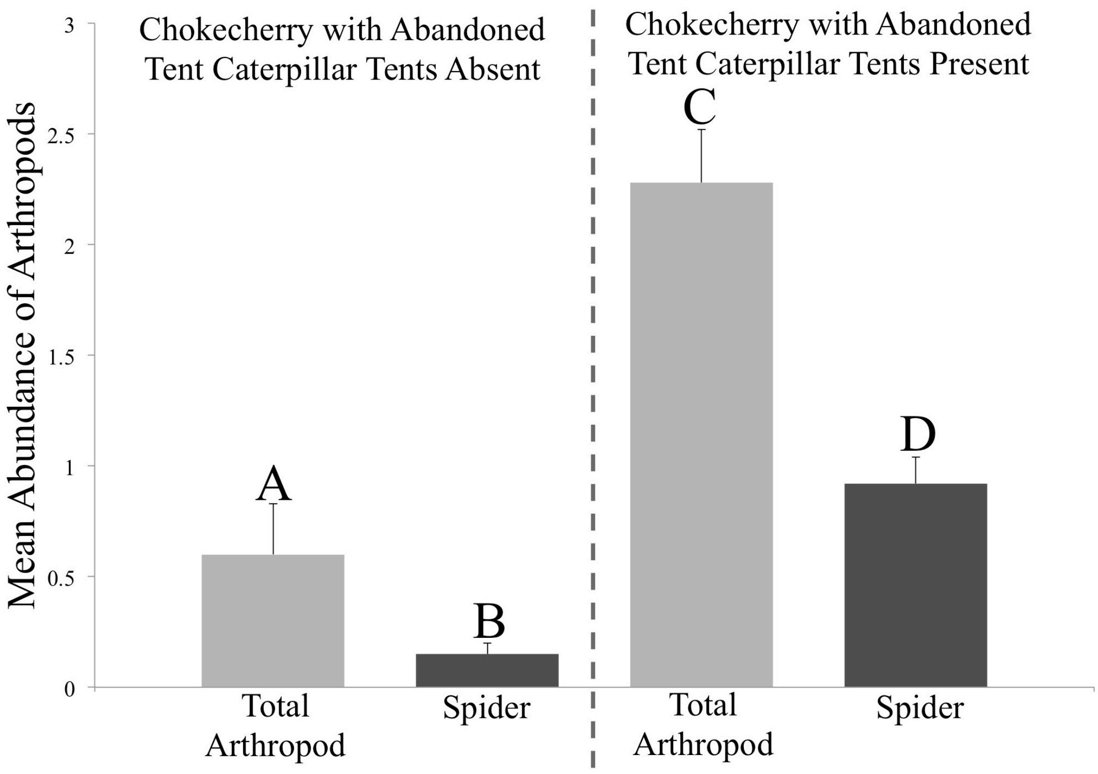


Figure 12. The mean abundance of total arthropods (light grey) and spiders (dark grey) on chokecherry plants with present or absent abandoned tent caterpillar tents in the August survey of arthropods on chokecherry. Significant differences between means are indicated with letters and error bars show ±1 SE.

Do tent caterpillars have long-term impacts on arthropod communities?

Chokecherry plants with an abandoned tent caterpillar tent present the previous year (mean rank=25.5) had more arthropods on them than shrubs with an abandoned tent caterpillar tent absent (mean rank=15.5; Z=3.6, N=40, p=0.0004), were more likely to have any arthropods present (χ^2=16.67, df=1, N=40, p<0.0001; Figure 13 A), and had a greater abundance of spiders on them (Z=3.1, N=40, p=0.002; Figure 13 B). We did not find any arthropods on the shrubs with a tent caterpillar tent absent the previous year (Figure 13). There were likely some arthropods on other parts of these shrubs, but they did not fall into the collection area.

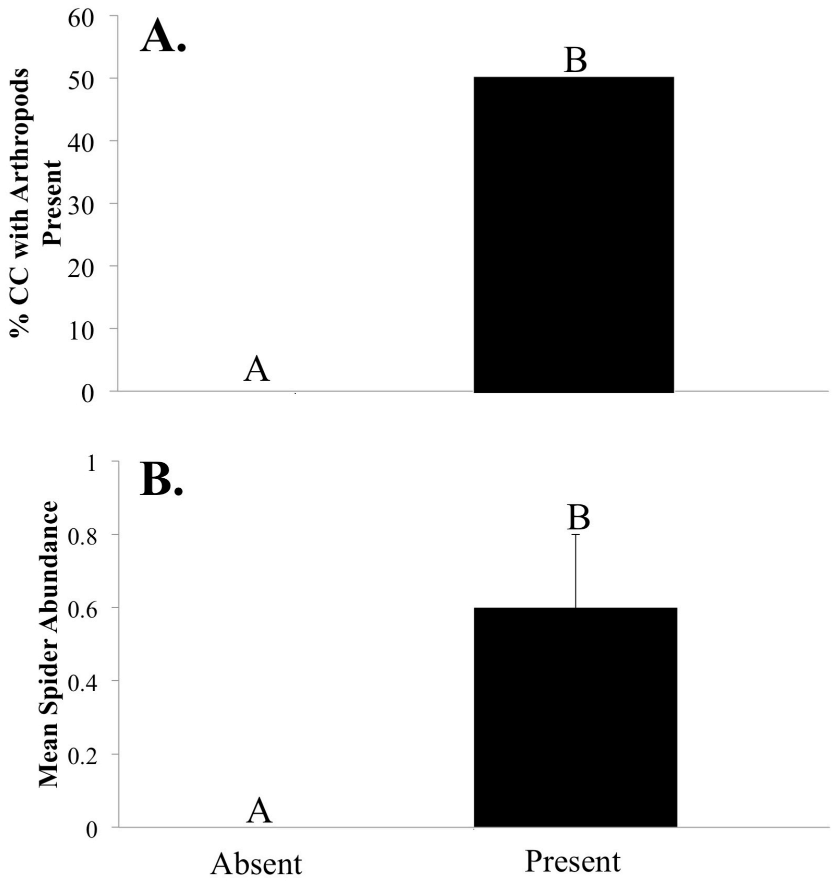
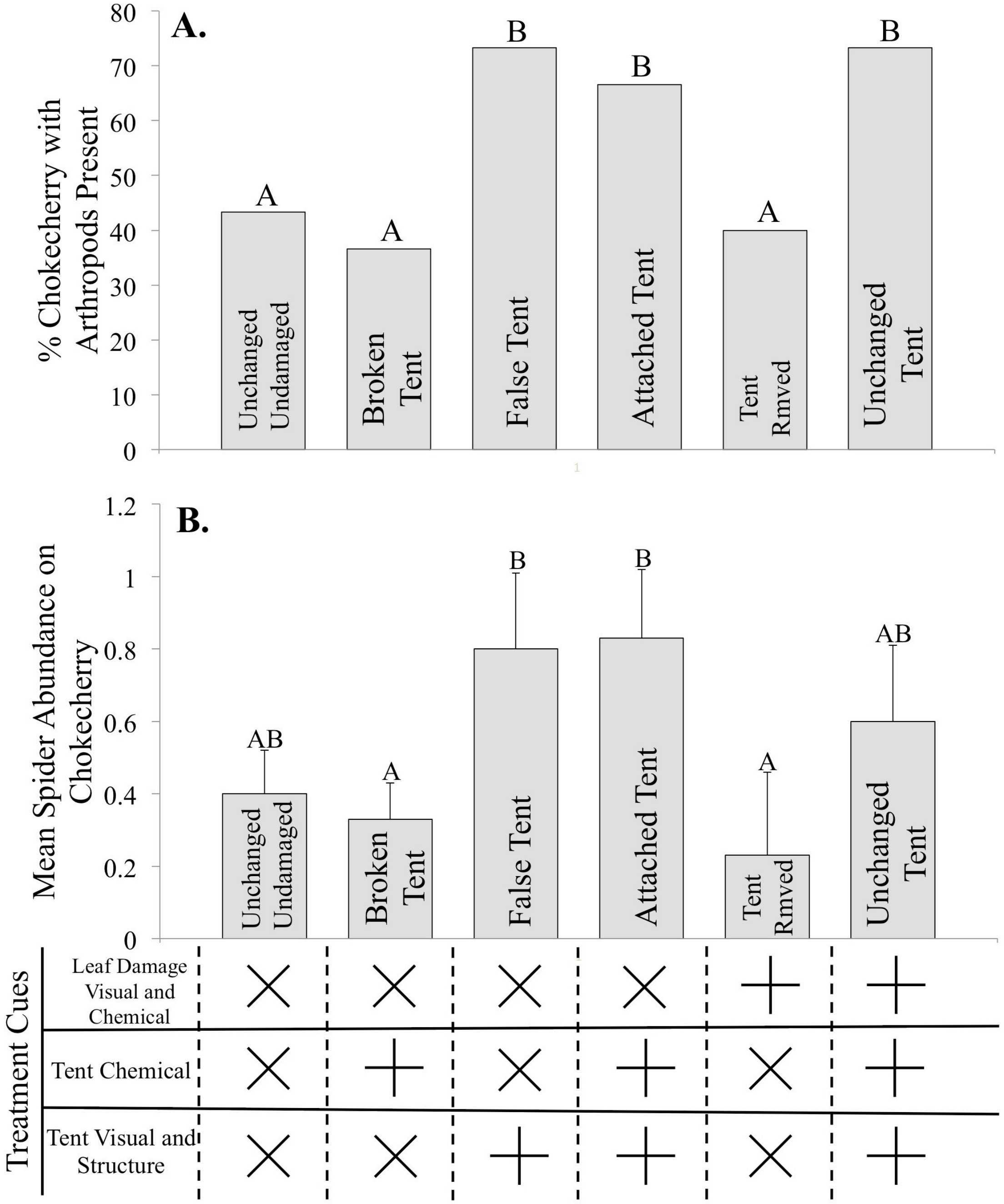


Figure 13. Percent of chokecherry with arthropods present (A) and mean spider abundance (B) in a survey of chokecherry one year after tent caterpillar were either present or absent on the shrubs. Significant differences between means are indicated with letters and error bars show ±1 SE.

How do tent caterpillars alter their host plant's arthropod community?

The treatments with tent visual cues and tent structure (unchanged tent, attached tent, and false tent treatments) were significantly more likely to have arthropods present (χ^2=18.27, df=5, N=180, p=0.0026; Figure 5), had greater arthropod abundance ($F_{5,180}$ =5.34, p=0.0002; unchanged tent=1.7±0.3, attached tent=2.0±0.3, false tent=1.7±0.3, unchanged undamaged=0.7±0.3, tent removed=0.6±0.3, and broken tent=0.6±0.3), and had greater spider abundance ($F_{5,180}$ =2.52, p=0.032; Figure 5) than the unchanged undamaged, tent removed, and the broken tent treatments (Appendix table 4).



Leaf Damage Visual and Chemical	X	X	X	X	+	+
Tent Chemical	X	+	X	+	X	+
Tent Visual and Structure	X	X	+	+	X	+

Figure 14. Percent of chokecherry with arthropods present and mean spider abundance in a community survey following the manipulation of cues created by tent caterpillars. Treatment names are written on the bars: chokecherries with no tent caterpillar damage and no tent treatment (unchanged undamaged treatment), chokecherries with no tent caterpillar damage that we covered in broken-apart tent caterpillar tents (broken tent treatment), chokecherries with no tent caterpillar damage with false wool tents attached (false tent treatment), chokecherries with no tent caterpillar damage to which we attached whole tent caterpillar tents (attached tent treatment), chokecherries with tent caterpillar damage and their tents removed (tent removed treatment), and chokecherries with both tent caterpillar damage and tents (unchanged tent treatment). Presence or absence of leaf damage visual and chemical cues, tent chemical cues, and tent visual cues and tent structure are recorded below the two graphs. Plus marks (+) indicate the presence of a cue and x marks (X) indicate the absence of a cue. Significant differences between means are indicated with letters and error bars show ±1 SE.

Discussion

Tent caterpillars act as ecosystem engineers by increasing the number of arthropods on their host plants. All of our surveys showed that plants with abandoned tent caterpillar tents were both more likely to have arthropods on them and had a greater total abundance of arthropods than plants with tent caterpillar tents absent. In July, we did not find a difference in the arthropod community between shrubs that had tent caterpillars present or absent earlier in the season, but tents account for most of the variation in arthropod count and we did not collect tents in July. In the August survey, tent caterpillar damage and tents primarily increased the abundance of predators, particularly spiders. Although greater numbers of predators are often linked to lower numbers of prey animals (Hodkinson et al. 2001), we did not find a corresponding change in the herbivore abundance with the increase in predator abundance. We may have found this result because, although shrubs with tents had more predators, they also have greater structural complexity, which is associated with higher numbers of herbivores (Lill and Marquis 2003). If the higher structural complexity increased the number of herbivores and then the higher number of predators consumed a similar number of herbivores, we would not expect to record a difference in herbivore abundance. We expect that if predators were excluded from shrubs with an abandoned tent caterpillar tent, then we would observe an even greater abundance of herbivores than we recorded. These potential interactions may mean that we have underestimated the importance of tent caterpillars as ecosystem engineers.

Abandoned tent caterpillar tents continued to alter the abundance of arthropods on their host plants at least a year after the tents were initially established. These plants lacked many of the herbivore cues that they had during the growing season that they were constructed. They no longer had the same leaves as the previous year, all of the leaves with structural or chemical changes caused by tent caterpillars were gone, and the tents were exposed to a year of weathering. Many of the volatile cues that plants produce after herbivory attract predators and parasitoids to an herbivore feeding on that plant (Agrawal 2011). It is therefore unlikely that the host plants were still producing volatile cues to attract the herbivores' natural enemies. In addition, the tents themselves became smaller by losing additional layers of silk and becoming more "felted" over the winter months, thereby reducing their internal shelter. However, we still found greater abundance of arthropods on shrubs with abandoned tent caterpillar tents than on shrubs without abandoned tent caterpillar tents and found similar orders of insects in our spring tents as in our July tents. These tents were present on the shrubs before spring insects emerged, leading to potential priority effects (Weslien et al. 2011, Miller-Pierce and Preisser 2012) from the organisms that can colonize the tents. The majority of the organisms we collected from the tents were spiders, which can exert strong top-down effects on arthropod communities (Hodkinson et al. 2001). In addition, solitary bees built nests inside the tent. Solitary bees are of interest to farmers for their potential as alternative pollinators (Wood et al. 2017) and thus tents could be used to promote bee presence near crops. The greater number of arthropods in the tent shrubs demonstrates that herbivorous insects can have long-lasting effects on arthropod communities and suggests that spiders, and perhaps other arthropods, may use the tents for their structure rather than because of other changes to the host plant as a whole. To our knowledge, shelter-building herbivores have never before been shown to have ecosystem engineering impacts that extend between years.

Many of the spiders that we collected on the shrubs with an abandoned tent caterpillar tent can be expected to have long-term effects on the arthropod community of chokecherry because they had established webs incorporated into the tent caterpillar tents and spiders invest energy in their webs (Eberhard 1988, Opell 1997, Kawamoto and Japyassu 2008, Anotaux et al. 2012). Spiders may preferentially use tent caterpillar tents as shelters because insect leaf shelters and tents alter the microclimate on plants (Alonso 1997, Ruf and Fiedler 2002, Fitzgerald et al. 2012) and other arthropods may also use insect-built shelter for protection from the elements (Cornelissen et al. 2016), potentially increasing the likelihood of catching prey. Spiders may also have built their webs in this location so that they are less visible to prey (Craig and Freeman 1991) or because the chemical cues produced by spiders (Rypstra et al. 2007) may be masked by the chemical cues from the tent. This long-term use of tents shows that spiders and other arthropods may gain a fitness benefit from using these tents for shelter.

Tent caterpillars are ecosystem engineers because the architectural component of tent caterpillar tents plays the greatest role in attracting and keeping arthropods, particularly spiders, on chokecherries. When we manipulated the chemical and structural cues on chokecherry shrubs, we found that the tent structure treatments were both more likely to have arthropods present on them and had more total arthropods on average compared with both the tent chemical and the leaf chemical cue treatments. Despite chemosensory cues often being the focus of studies of insect host finding (Reeves 2011), neither the presence of tent chemosensory cues nor the presence of leaf damage cues played a role in arthropod presence on these host plants. More consideration should be given to the impact that host plant structure that has been altered by arthropods has on keeping other arthropods, particularly natural enemies, on host plants. The microhabitat created by the structure of the tents most likely increased the overall fitness of the organisms using it by moderating temperature, moisture, and solar radiation (Alonso 1997, Ruf and Fiedler 2002, Fitzgerald et al. 2012). The tent may also have allowed prey animals to hide from or escape from natural enemies (Gingras et al. 2002, Gols et al. 2005, Obermaier et al. 2008). These results demonstrate that tent caterpillars are acting as structural ecosystem engineers and that the changes they cause in arthropod communities are not due to feeding effects.

Tent caterpillars act as structural ecosystem engineers by building long-lasting tents with complex internal structure. These tents alter chokecherry communities past the end of the growing season in which they were created, showing longer-lasting effects by a structure-building herbivore on arthropod communities than have previously been demonstrated. Our results may have applied implications, as land managers, farms and, anecdotally, private citizens may seek to remove tent caterpillars, thereby inadvertently changing the arthropod community on their plants, including decreasing the number of valuable predators and pollinators. We show that shelter-building insects can have long-term effects on their communities by acting as ecosystem engineers.

REFERENCES

Abdala-Roberts, L., A. A. Agrawal, and K. A. Mooney. 2012. Ant-aphid interactions on *Asclepias syriaca* are mediated by plant genotype and caterpillar damage. Oikos 121:1905–1913.

Agrawal, A. A. 2000. Specificity of induced resistance in wild radish: causes and consequences for two specialist and two generalist caterpillars. Oikos 89:493–500.

Agrawal, A. A. 2011. Current trends in the evolutionary ecology of plant defence. Functional Ecology 25:420–432.

Alba, C., M. D. Bowers, D. Blumenthal, and R. A. Hufbauer. 2014. Chemical and mechanical defenses vary among maternal lines and leaf ages in Verbascum thapsus L. (Scrophulariaceae) and reduce palatability to a generalist insect. PloS one 9:e104889.

Alonso, C. 1997. Choosing a place to grow. Importance of within-plant abiotic microenvironment for *Yponomeuta mahalebella*. Entomologia Experimentalis et Applicata 83:171–180.

Anotaux, M., J. Marchal, N. Châline, L. Desquilbet, R. Leborgne, C. Gilbert, and A. Pasquet. 2012. Ageing alters spider orb-web construction. Animal Behaviour 84:1113–1121.

Awmack, C. S., and S. R. Leather. 2002. Host plant quality and fecundity in herbivorous insects. Annual Review of Entomology 47:817–844.

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 70:277–282.

Bernays, E. A. 1998. Evolution of insect feeding behavior in herbivores: success seen as different ways to eat without being eaten. BioScience 48:35–44.

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 101:555–562.

Buchanan, A. L., S. L. Hermann, M. Lund, and Z. Szendrei. 2017. A meta-analysis of non-consumptive predator effects in arthropods: the influence of organismal and environmental characteristics. Oikos 126:1233–1240.

Bultman, T. L., and S. H. Faeth. 1986. Experimental evidence for intraspecific competition in a Lepidopteran leaf miner. Ecology 67:442–448.

Cadogan, B. L., and R. D. Scharbach. 2005. Effects of a kaolin-based particle film on oviposition and feeding of gypsy moth (Lep., Lymantriidae) and forest tent caterpillar (Lep., Lasiocampidae) in the laboratory. Journal of Applied Entomology 129:498–504.

Cohen, J. 1988. Statistical Power Analysis for the Behavioral Sciences. Lawrence Erlbaum Associates, New Jersey, USA.

Coley, P., and J. Barone. 1996. Herbivory and plant defenses. Annual Review of Ecology and Systematics 27:305–335.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. Ecology 42:710–723.

Constant, B., S. Grenier, G. Febvay, and G. Bonnot. 1996. Host Plant Hardness in

Oviposition of Macrolophus caliginosus (Hemiptera: Miridae). Journal of economic entomology 89:1446–1452.

Cornelissen, T., F. Cintra, and J. C. Santos. 2016. Shelter-building insects and their role as ecosystem engineers. Neotropical Entomology 45:1–12.

Craig, C. L., and C. R. Freeman. 1991. Effects of predator visibility on prey encounter: A case study on aerial web weaving spiders. Behavioral Ecology and Sociobiology 29:249–254.

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 115:161–170.

Derner, J. D., W. K. Lauenroth, P. Stapp, and D. J. Augustine. 2009. Livestock as ecosystem engineers for grassland bird habitat in the Western Great Plains of North America. Rangeland Ecology & Management 62:111–118.

Eberhard, W. G. 1988. Behavioral flexibility in orb web construction: effects of supplies in different silk glands and spider size and weight. The Journal of Arachnology 16:295–302.

Faeth, S. H. 1986. Indirect interactions between temporally separated herbivores mediated by the host plant. Ecology 67:479–494.

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

Finke, D. L., and R. F. Denno. 2002. Intraguild predation diminish in complex-structured vegetation: Implications for prey supression. Ecology 83:643–652.

Fitzgerald, T. D. 1995. The Tent Caterpillars. Cornell University Press, Ithaca.

Fitzgerald, T. D., S. Miller, and M. Smith. 2012. Thermal properties of the tent of early instar colonies of the eastern tent caterpillar, *Malacosoma americanum* (Lepidoptera: Lasiocampidae). Journal of Thermal Biology 37:615–624.

Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity and Conservation 1244:1221–1244.

Gause, G. F. 1934. The Struggle for Existence. Williams & Wilkins, Baltimore, USA.

Gingras, D., P. Dutilleul, and G. Boivin. 2002. Modeling the impact of plant structure on host-finding behavior of parasitoids. Oecologia 130:396–402.

Gols, R., T. Bukovinszky, L. Hemerik, J. A. Harvey, J. C. Van Lenteren, and L. E. M. Vet. 2005. Reduced foraging efficiency of a parasitoid under habitat complexity: Implications for population stability and species coexistence. Journal of Animal Ecology 74:1059–1068.

Gotoh, T., M. Koyama, Y. Hagino, and K. Doke. 2011. Effect of leaf toughness and temperature on development in the lilac pyralid, *Palpita nigropunctalis* (Bremer) (Lepidoptera: Crambidae). Journal of Asia-Pacific Entomology 14:173–178.

Griffith, D. M., and T. L. Poulson. 1993. Mechanisms and consequences of intraspecific competition in a carabid cave beetle. Ecology 74:1373–1383.

Gross, P. 1993. Insect behavioral and morphological defenses against parasitoids. Annual Review of Entomology 38:251–273.

Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. The American Nautralist 140:539–572.

Harrison, S., and R. Karban. 1986. Effects of an early-season folivorous moth on the success of a later-season species, mediated by a change in the quality of the shared host, *Lupinus arboreus* Sims. Oecologia 69:354–359.

Hastings, A., J. E. Byers, J. A. Crooks, K. Cuddington, C. G. Jones, J. G. Lambrinos, T. S. Talley, and W. G. Wilson. 2007. Ecosystem engineering in space and time. Ecology letters 10:153–64.

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

Hodkinson, I. D., S. J. Coulson, and J. Harrison. 2001. What a wonderful web they weave: spiders, nutrient capture and early ecosystem development in the high Arctic–some counter-intuitive ideas on community assembly. Oikos 95:349–352.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197–229.

Janzen, D. H. 1973. Host plants as islands. II. Competition in evolutionary and contemporary time. The American Naturalist 107:786–790.

Jeffries, M. J., and J. H. Lawton. 1984. Enemy free space and the structure of ecological communities. Biological Journal of the Linnean Society 23:269–286.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

Jouquet, P., J. Dauber, J. Lagerlöf, P. Lavelle, and M. Lepage. 2006. Soil invertebrates as ecosystem engineers: Intended and accidental effects on soil and feedback loops. Applied Soil Ecology 32:153–164.

Kaitaniemi, P., K. Ruohomäki, V. Ossipov, E. Haukioja, and K. Pihlaja. 1998. Delayed induced changes in the biochemical composition of host plant leaves during an insect outbreak. Oecologia 116:182–190.

Kaitaniemi, P., K. Ruohomaki, T. Tammaru, and E. Haukioja. 1999. Induced resistance of host tree foliage during and after a natural insect outbreak. Journal of Animal Ecology 68:382–389.

Kaplan, I., and R. F. Denno. 2007. Interspecific interactions in phytophagous insects revisited: A quantitative assessment of competition theory. Ecology Letters 10:977–994.

Karban, R. 1989. Community organization of *Erigeron glaucus* folivores: Effects of competition, predation, and host plant. Ecology 70:1028–1039.

Karban, R., and I. T. Baldwin. 1997. Interspecific Interactions: Induced Responses to Herbivory. The University of Chicago Press, Chicago, IL, USA.

Kawamoto, T. H., and H. F. Japyassu. 2008. Tenacity and silk investment of two orb weavers: Considerations about diversification of Araneoidea. The Journal of Arachnology 36:418–424.

Klomp, H. 1964. Intraspecific competition and the regulation of insect numbers. Annual Review of Entomology 17:17–40.

Langellotto, G. A., and R. F. Denno. 2006. Refuge from cannibalism in complex-structured habitats: Implications for the accumulation of invertebrate predators. Ecological Entomology 31:575–581.

Lehtilä, K., and E. Boalt. 2008. The Use and Usefulness of Artificial Herbivory in Plant-Herbivore Studies. Springer Berlin Heidelberg, Berlin.

Lensing, J. R., and D. H. Wise. 2006. Predicted climate change alters the indirect effect of predators on an ecosystem process. Proceedings of the National Academy of Sciences of the United States of America 103:15502–15505.

Lill, J. T., and R. J. Marquis. 2003. Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. Ecology 84:682–690.

Lill, J. T., and R. J. Marquis. 2007. Ecosystem engineers: Plants to protists. Academic Press.

Lill, J. T., R. J. Marquis, M. A. Walker, and L. Peterson. 2007. Ecological consequences of shelter sharing by leaf-tying caterpillars. Entomologia Experimentalis et Applicata 124:45–53.

Loewy, K. J., A. L. Flansburg, K. Grenis, M. 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 67:196–205.

Long, J. D., R. S. Hamilton, and J. L. Mitchell. 2007. Asymmetric competition via induced resistance: Specialist herbivores indirectly suppress generalist preference and populations. Ecology 88:1232–40.

MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist 101:377–385.

Majak, W., R. E. McDiarmid, and J. W. Hall. 1981. The cyanide potential of saskatoon serviceberry (*Amelanchier alnifolia*) and chokecherry (*Prunus virginiana*). Canadian Journal of Animal Science 61:681–686.

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 3:1–8.

Marquis, R. J., and J. T. Lill. 2010. Impact of plant architecture versus leaf quality on attack by leaf-tying caterpillars on five oak species. Oecologia 163:203–13.

Matsuki, S., Y. Sano, and T. Koike. 2004. Chemical and physical defence in early and late leaves in three heterophyllous birch species native to northern Japan. Annals of Botany 93:141–147.

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 17:303–310.

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 31:20–31.

Miller-Pierce, M. R., and E. L. Preisser. 2012. Asymmetric priority effects influence the success of invasive forest insects. Ecological Entomology 37:350–358.

Morris, R. J., O. T. Lewis, and H. C. J. Godfray. 2005. Apparent competition and insect community structure: towards a spatial perspective. Annales Zoologici Fennici 42:449–462.

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 101:18048–18052.

Nelson, X. J., and R. R. Jackson. 2014. Timid spider uses odor and visual cues to actively select protected nesting sites near ants. Behavioral Ecology and Sociobiology 68:773–780.

Norton, A. P., G. English-Loeb, and E. Belden. 2001. Host plant manipulation of natural enemies: Leaf domatia protect beneficial mites from insect predators. Oecologia

126:535–542.

Nykanen, H., 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 104:247–268.

Obermaier, E., A. Heisswolf, J. Poethke, B. Randlkofer, and T. Meiners. 2008. Plant architecture and vegetation structure: Two ways for insect herbivores to escape parasitism. European Journal of Entomology 105:233–240.

Opell, B. D. 1997. The material cost and stickiness of capture threads and the evolution of orb-weaving spiders. Biological Journal of the Linnean Society 62:443–458.

Powell, J. A., and P. A. Opler. 2009. Moths of Western North America. University of California Press, Berkeley, CA.

Prokopy, R. J., and E. D. Owens. 1983. Visual detection of plants by herbivorous insects. Annual Review of Entomology 28:337–364.

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 158:854–863.

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 125:218–228.

Reeves, J. L. 2011. Vision should not be overlooked as an important sensory modality for finding host plants. Environmental Entomology 40:855–863.

Renwick, J. A. A. 1989. Chemical ecology of oviposition in phytophagous insects.

Experientia 45:223–228.

de Rijk, M., M. Dicke, and E. H. Poelman. 2013. Foraging behaviour by parasitoids in multiherbivore communities. Animal Behaviour 85:1517–1528.

Robert, C. A. M., M. Erb, B. E. Hibbard, B. Wade French, C. Zwahlen, and T. C. J. Turlings. 2012. A specialist root herbivore reduces plant resistance and uses an induced plant volatile to aggregate in a density-dependent manner. Functional Ecology 26:1429–1440.

Ruf, C., and K. Fiedler. 2002. Tent-based thermoregulation in social caterpillars of *Eriogaster lanestris* (Lepidoptera: Lasiocampidae): Behavioral mechanisms and physical features of the tent. Journal of Thermal Biology 27:493–501.

Rypstra, A. L., J. M. Schmidt, B. D. Reif, J. DeVito, and M. H. Persons. 2007. Tradeoffs involved in site selection and foraging in a wolf spider: Effects of substrate structure and predation risk. Oikos 116:853–863.

Schmid, J. M., P. A. Farrar, and I. Ragenovich. 1981. Length of western tent caterpillar egg masses and diameter of their associated stems. Great Basin Naturalist 41:465–466.

Schmidt, M. H., I. Roschewitz, C. Thies, and T. Tscharntke. 2005. Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. Journal of Applied Ecology 42:281–287.

Schmitz, O. 2003. Top predator control of plant biodiversity and productivity in an old-field ecosystem. Ecology Letters:156–163.

Schmitz, O. J. 2009. Effects of predator functional diversity on grassland ecosystem function. Ecology 90:2339–2345.

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 78:1388–1399.

Schoonhoven, L. M., J. J. A. van Loon, and M. Dicke. 2005. Insect-Plant Biology. 2nd edition. Oxford University Press, New York, USA.

Schultz, J. C., and I. T. Baldwin. 1982. Oak leaf quality declines in response to defoliation by gypsy moth larvae. Science 217:149–151.

Shear, W. A. 1986. Spiders: Webs, Behavior, and Evolution. Stanford University Press.

Shiojiri, K., J. Takabayashi, S. Yano, and A. Takafuji. 2002. Oviposition preferences of herbivores are affected by tritrophic interaction webs. Ecology Letters 5:186–192.

Sponberg, S., J. P. Dyhr, R. W. Hall, and T. L. Daniel. 2015. Luminance-dependent visual processing enables moth flight in low light. Science 348:1245–1248.

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 6:1893–1896.

Svanbäck, R., and D. I. Bolnick. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proceedings of the Royal Society B: Biological Sciences 274:839–844.

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 128:34–40.

Thompson, J. N. 1988. Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. Entomologia

Experimentalis et Applicata 47:3–14.

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 153:270–275.

Tuda, M., L. H. Wu, N. Yamada, C. P. Wang, W. J. Wu, S. Buranapanichpan, K. Kagoshima, Z. Q. Chen, K. K. Teramoto, B. R. Kumashiro, and R. Heu. 2014. Host shift capability of a specialist seed predator of an invasive plant: Roles of competition, population genetics and plant chemistry. Biological Invasions 16:303–313.

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 92:4169–4174.

Uesugi, A., K. Morrell, E. H. Poelman, C. E. Raaijmakers, A. Kessler, and M. Heil. 2016. Modification of plant-induced responses by an insect ecosystem engineer influences the colonization behaviour of subsequent shelter-users. Journal of Ecology 104:1096–1105.

Valdovinos, F. S., P. Moisset de Espanés, J. D. Flores, and R. Ramos-Jiliberto. 2013. Adaptive foraging allows the maintenance of biodiversity of pollination networks. Oikos 122:907–917.

VanNimwegen, R. E., J. Kretzer, and J. F. Cully. 2008. Ecosystem engineering by a colonial mammal: How prairie dogs structure rodent communities. Ecology 89:3298–3305.

van Veen, F. J., R. J. Morris, and H. C. J. Godfray. 2006. Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. Annual Review of Entomology 51:187–208.

Viswanathan, D. V, A. J. T. Narwani, and J. S. Thaler. 2005. Specificity in induced plant responses shapes patterns of herbivore occurrence on Solanum dulcamara. Ecology 86:886–896.

Waage, J. K. 1978. Arrestment responses of the parasitoid, Nemeritis canescens, to a contact chemical produced by its host, Plodia interpunctella. Physiological Entomology 3:135–146.

Wagner, D. L. 2005. Caterpillars of Eastern North America. Princeton University Press, New Jersey, USA.

Weiss, M. R. 2003. Good housekeeping: Why do shelter-dwelling caterpillars fling their frass? Ecology Letters 6:361–370.

Weslien, J., L. B. Djupström, M. Schroeder, and O. Widenfalk. 2011. Long-term priority effects among insects and fungi colonizing decaying wood. Journal of Animal Ecology 80:1155–1162.

Williams, K. S., and J. H. Myers. 1984. Previous herbivore attack of red alder may improve food quality for fall webworm larvae. Oecologia 63:166–170.

Wink, M. 2010. Introduction: Biochemistry, physiology and ecological functions of secondary metabolites. Annual Plant Reviews 40:1–19.

Wood, T. J., J. M. Holland, and D. Goulson. 2017. Providing foraging resources for solitary bees on farmland: current schemes for pollinators benefit a limited suite of species. Journal of Applied Ecology 54:323–333.

Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. Annual Review of Ecology and Systematics 25:443–446.

Wright, J. P., and C. G. Jones. 2006. The concept of organisms as ecosystem engineers ten years on: Progress, limitations, and challenges. BioScience 56:203.

Wright, J. P., C. G. Jones, and A. S. Flecker. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132:96–101.

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 101:410–417.

Van Zandt, P. A., and A. A. Agrawal. 2004a. Community-wide impacts of herbivore-induced plant responses in milkweed (*Asclepias syriaca*). Ecology 85:2616–2629.

Van Zandt, P. A., and A. A. Agrawal. 2004b. Specificity of induced plant responses to specialist herbivores of the common milkweed *Asclepias syriaca*. Oikos 2:401–409.

APPENDIX

Appendix Table 1. Mean host plant quality values (±1 SE) of chokecherry leaves with tent caterpillar larvae absent and tent caterpillar larvae present one year before leaves were collected. Leaves were tested in the spring of 2016 for %water, toughness (g), hydrogen cyanide (HCN ppm), percent carbon (%C), and percent nitrogen (%N). Bold indicates values that differed significantly between treatments.

Treatment	**%Water**	**Toughness**	**HCN**	**%C**	**%N**
Tent Caterpillar Absence	0.028±0.002	**41.34±1.25**	753.57±30.63	48.18±0.25	2.51±0.08
Tent Caterpillar Presence	0.028±0.002	**47.16±2.01**	769.23±39.32	48.40±0.24	2.40±0.06

Appendix Table 2. Mean leaf host plant quality values with ±1 SE and significance indicated with asterisks. Spring and Late Summer are the time points that we collected the leaves for the analysis. Prior fall webworms and tent caterpillar absence and presence indicate if the plants had larvae feeding on them the in the past. Concurrent fall webworm damaged plants are those that fall webworms were feeding on while the leaves were collected.

Treatment	Water Content (mg/cm)	Toughness (g)	HCN (ppm)	%C	%N
Spring					
Prior Fall Webworm Absence	0.028±0.0016	41.34±1.25	753.6±30.6	48.18±0.25*	2.51±0.08
Prior Fall Webworm Presence	0.031±0.0024	44.28±4.93	687.5±81.2	49.35±0.47*	2.48±0.17
Late Summer					
Prior Tent Caterpillar Absence	0.030±0.0020	59.12±3.53	619.6±55.0	49.90±0.38*	1.84±0.06
Prior Tent Caterpillar Presence	0.032±0.0025	60.69±2.44	618.5±52.0	49.09±0.36*	1.79±0.06
Concurrent Fall Webworm Damage	0.031±0.0026	57.47±3.03	671.1±49.9	49.16±0.29*	1.88±0.06

Appendix Table 3. Number of chokecherry plants surveyed at our four field sites in the July and August surveys in 2014. Present treatments were shrubs that tent caterpillar larvae fed and constructed a tent on in spring 2014 and absent treatments were shrubs that tent caterpillar larvae did not feed on or construct a tent on in spring 2014.

	Treatment	Betasso Preserve	Boulder Canyon	Walker Ranch	Centennial Cone Park	Total
July	Present	8	14	4	8	34
	Absent	6	12	4	9	31
August	Present	14	15	6	15	50
	Absent	9	14	6	11	40

Appendix Table 4. Mean abundance with SE of arthropods by order in the six treatments in the cue manipulation experiment. Treatments are: chokecherries with no tent caterpillar damage and no tent treatment (unchanged undamaged treatment), chokecherries with no tent caterpillar damage that we covered in broken-apart tent caterpillar tents (broken tent treatment), chokecherries with no tent caterpillar damage with false wool tents attached (false tent treatment), chokecherries with no tent caterpillar damage to which we attached whole tent caterpillar tents (attached tent treatment), chokecherries with tent caterpillar damage and their tents removed (tent removed treatment), and chokecherries with both tent caterpillar damage and tents (unchanged tent treatment).

Arthropod Order	**Unchanged Undamaged**	**Broken Tent**	**False Tent**	**Attached Tent**	**Tent Removed**	**Unchanged Tent**
Araneae	0.4±0.1	0.3±.1	0.8±0.2	0.8±0.2	0.2±0.09	1.2±0.2
Coleoptera	0.03±0.3	0.03±0.03	0.3±0.2	0.3±0.1	0±0	0.3±0.2
Dermaptera	0±0	0.07±0.07	0.03±0.03	0.4±0.2	0±0	0.2±0.1
Diptera	0±0	0±0	0±0	0±0	0.03±0.03	0.07±0.05
Hemiptera	0.1±0.07	0.07±0.04	0.1±0.06	0.1±0.06	0.1±0.07	0.1±0.06
Hymenoptera	0.1±0.06	0±0	0.03±0.03	0.1±0.06	0.07±0.04	0.1±0.08
Lepidoptera	0.03±0.03	0.03±0.03	0.2±0.07	0.07±0.05	0.07±0.04	0±0
Orthoptera	0±0	0.03±0.03	0.03±0.03	0.07±0.05	0±0	0.07±0.05
Thysanoptera	0.03±0.03	0±0	0±0	0±0	0.03±0.03	0±0
Phasmatodea	0±0	0.03±0.03	0±0	0±0	0.03±0.03	0±0