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Research article

Bottom-up mediation of an ant-membracid mutualism: effects from different host plants

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Abstract. The relationship between the membracid, *Publilia modesta*, and the tending ant, *Formica obscuripes*, was either a mutualism or commensalism depending on the host plant species. Experimental manipulation of the presence of ants in two different years indicated that the presence of ants had a positive effect on nymph numbers on both host plants, *Chrysothamnus viscidiflorus* and *Wyethia* spp. However, *Wyethia* spp. senesced before membracid nymphs reached adulthood, causing extensive mortality of membracids. In contrast, *C. viscidiflorus* plants senesced after nymphs had developed into adults. The increased number of nymphs in the presence of ants translated into more new adults on *C. viscidiflorus*, but not on *Wyethia* spp. Poor host plant choices may render the presence of ants irrelevant for such insects on some host plants. Being a host plant generalist may lead to significant variability in the outcomes of mutualistic interactions.

Key words: ants, bottom-up, conditional outcomes, host plants, membracids, mutualism, *Publilia modesta*, RMBL

Introduction

The evolutionary trajectory of mutualisms will depend in part upon the extent and manner in which the outcome of the interaction varies in space and time (Bronstein, 1994). Partners may invest resources in a relationship even when a partner is not present (Stadler *et al.*, 2001), or under circumstances in which a partner is not effective. This lack of dependability, or conditionality, in the outcome of the mutualism will mean that there are times and places when investment of substantial resources in a mutualism may not be justified by the benefit received. As a result variability in the effect of one partner on another may tend to favor loose mutualisms in which the investment in the mutualism is limited and the mutualisms are facultative.

In a review of conditional outcomes in mutualisms, Bronstein (1994) predicted that outcomes are more likely to be conditional when a third species is

intimately involved in the mutualism. Work on mutualisms involving ants supports the hypothesis that third species affecting mutualisms in a top-down manner are important. The primary benefit of ants on their partners is protection from predation (Inouye and Taylor, 1979; Pierce, 1981; Cushman and Whitham, 1989; Bach, 1991; Del-Claro and Oliveira, 2000; Morales, 2001) and/or fungal parasitism (Bach, 1991). For this reason it is not surprising that there is empirical evidence that temporal variation in the density of predators generates variability in the strength of the positive effect of ants on their partners (Cushman and Whitham, 1989; Del-Claro and Oliveira, 2000).

Less intuitively, Cushman (1991) suggested that for herbivorous insects, bottom-up effects may mediate mutualisms. Indeed, ant-tended insects, e.g. aphids, scales, membracids, and lycaenid butterflies, typically spend their entire larval lives and sometimes their adult lives on a single host plant; to a large extent the host plant will create the environmental context in which an ant-insect mutualism occurs. Quite a few insects involved in ant-insect mutualisms are host plant generalists (Wood, 1984; Pierce and Elgar, 1985), raising the possibility that variation in host plant use may play an important role in mediating the outcome of ant-insect mutualisms. There is little empirical evidence, however, that host plants generate conditional outcomes (Cushman, 1991, although see Baylis and Pierce, 1991).

We tested the effect of host plants on the outcome of the interaction between the membracid, *Publilia modesta*, a generalist insect herbivore, and the tending ant, *Formica obscuripes*. While several studies have documented that the strength of this interaction varies significantly through time (Cushman and Whitham, 1989; Billick and Tonkel, 2003), these studies have been limited to studying *P. modesta* on one host plant. We experimentally manipulated the densities of ants on two different host plant species, *Chrysothamnus viscidiflorus* and *Wyethia* spp., in order to determine the extent to which the benefit of the ants on the membracids depended upon the host plant. Combining our experimental results with information from a previous study (Reithel, 2003) that examined the oviposition preferences of the membracids, we discuss the manner in which being a host plant generalist may affect variability in insect-ant mutualisms.

Materials and methods

Study site and species

Experiments were conducted in the Almont Triangle (elev. 2720 m) approximately 30 km southeast of the Rocky Mountain Biological Laboratory in Gothic, Gunnison Co., Colorado. The Almont Triangle is composed of relatively arid southwest facing meadows surrounded by aspen groves. Dominant

vegetation in meadows includes *Artemisia tridentata* (sagebrush), *Chrysothamnus* spp. (rabbitbrush), grasses, and herbaceous perennials.

Publilia modesta is a phytophagous ant-tended homopteran. At Almont Triangle *P. modesta* is most commonly tended by the ant, *Formica obscuripes*. Membracids excrete honeydew, which ants collect and consume. Ants benefit membracids by protecting them from predators including spiders, lacewing larvae, and coccinellids (Cushman and Whitham, 1989; Morales, 2001, pers. obs.) and by removing honeydew, which is thought to decrease sooty mold growth (McEvoy, 1979). *Publilia modesta* produces one generation per year at this site. In May and June, females lay eggs in midribs and stems of herbaceous and woody plants. At Almont Triangle, females oviposit on at least 6 genera: *Wyethia* spp., *Chrysothamnus viscidiflorus, Erigeron* sp., *Balsamorhiza sagittata*, *Helianthella quinquenervis*, and *Lupinus* sp. Nymphs hatch continuously over the course of about 3 weeks and feed on the host plant from which they emerged. Nymphs do not move from their host plant unless it begins to senesce, in which case they move onto nearby plants. *Publilia modesta* nymphs feed on at least 16 species of plants from four families: Asteraceae, Fabaceae, Polygonaceae, and Scrophulariaceae. Nymphs become adults in August and September. Both male and female adults overwinter at the roots of plants and mate in the spring.

At Almont Triangle, the three perennials, *Wyethia* spp., *Chrysothamnus viscidiflorus*, and *Balsamorhiza sagittata*, account for 76% of the host plants used by *P. modesta* (Reithel, 2003). Experiments were conducted with *Wyethia* spp. and *C. viscidiflorus*, but not *B. sagittata*. Limiting experiments to only two host plants allowed sufficient replication such that clear differences between species were detectable. *Balsamorhiza sagittata* was not used in experiments because it is the least common of the three hosts within the region. *Publilia modesta* does not feed on *B. sagittata* at any of four additional sites within 50 km of Almont Triangle, whereas *Wyethia* spp. and *C. viscidiflorus* are both used at additional sites (Reithel, unpublished data).

Wyethia spp., which includes *Wyethia arizonica* Gray and hybrids of *Wyethia arizonica* and *Wyethia amplexicaulis* (Nuttall) Nutall (Weber and Wittman, 1996), are herbaceous sunflowers with broad leaves. At Almont Triangle, plants bloom in late June/early July and most individuals have completely senesced by late August, roughly the same time that membracid nymphs become adults. *Chrysothamnus viscidiflorus* (Hooker) Nuttall, a small shrub, flowers in late July/early August and senesces in mid- to late-September.

Experimental design

During late June and early July of 2000, we setup an experiment with six treatments: two plant species (*C. viscidiflorus* and *Wyethia* spp.)×three ant

treatments (high abundance of ants, low abundance of ants, and no ants). These three ant treatments allowed us to test not only whether the presence of ants affected membracid survival on two hosts, but also whether that effect was consistent in locations of high and low ant abundance. At each of 24 colonies, all *Wyethia* spp. and *C. viscidiflorus* plants with membracids were included in the experiment as long as they were within approximately 3 m of a colony and met minimum size criteria: *Wyethia* spp. plants had at least three leaves and *C. viscidiflorus* plants were at least 10 cm tall. Plants receiving the same treatment at each colony were averaged making the total sample size 144 (24 colonies×6 treatments).

Ant abundance was manipulated by assembling a barrier (approximately 7 m long and 20 cm tall) made of aluminum flashing at each colony. We randomly determined the direction the barrier faced relative to each colony, buried approximately 5–10 cm of the aluminum barrier in the ground, and nailed the barrier in place. We cut vegetation away from the barrier and spread a 5 cm band of Tanglefoot (Tanglefoot Company, Grand Rapids, MI, USA) on the colony side of the barrier to prevent ants from climbing over the top. In this way, we created a wall around which ants had to travel in order to tend some of the membracids. In effect, plants on the side opposite from the colony were 'distanced' from the colony, thus reducing ant abundance. Besides decreasing ant abundance outside the barrier, the wall tended to funnel ants in the opposite direction resulting in increased ant abundance on the colony side of the barrier. Ants were completely excluded from at least two plants per colony by placing aluminum cylinders (approximately 10 cm tall and 30 cm in diameter) in the ground around individual plants. The outside rim of cylinders was spread with Tanglefoot and nearby vegetation was trimmed to prevent ants from using vegetation to climb over cylinders. Treatments were maintained at least every 2 weeks.

Plants were surveyed every two weeks from July 1 to September10, 2000, for a total of six surveys. We counted the number of adults in each survey. As soon as new adults began to emerge, they were marked with a non-toxic paint pen (Hunt Corporation, Statesville, NC, USA). The number of new adults was calculated as the cumulative total of unmarked adults from each week, not including adults present at the beginning of the experiment. We counted the number of nymphs in every survey except survey five. We noted whether plants had senesced in every survey except surveys one and five. Plants were considered senesced if they were completely dried up and had no suitable substrate upon which nymphs could feed.

In 2001, we setup a similar experiment with four treatments: two plant species (*C. viscidiflorus* and *Wyethia* spp.)×two ant treatments (presence and absence of ants). We only used two ant treatments in 2001 because manipulating ant abundance in 2000 did not significantly affect per capita ant tending.

The four treatments were replicated at each of 35 ant colonies for a total of 140 experimental units. Plants used in the experiment were within approximately 5 m of an ant colony and met minimum size criteria: *Wyethia* spp. had at least four leaves and *C. viscidiflorus* were at least 15 cm tall. Ant treatments were randomly assigned to plants. Cylinders made of aluminum flashing (approximately 10 cm tall and 30 cm in diameter) were assembled around all plants during June 2001. Flashing used to exclude ants was a complete cylinder, while flashing around plants with ants had an opening in the cylinder. By assembling cylinders around all plants, we controlled for the effects of the aluminum cylinder, while still allowing ants to access some plants. As above, Tanglefoot was applied to the rims of half the cylinders to exclude ants. A small amount of Tanglefoot was also applied to open cylinders around plants with ants. Vegetation around all plants was trimmed. Treatments were maintained on a weekly basis throughout the summer.

Plants were surveyed every 1–2 weeks from 26 June to 5 September 2001, for a total of nine surveys. The same data were collected in 2001 as in 2000. For surveys 1–3, 5, 7, and 9, we recorded the number of nymphs and whether or not host plants had senesced. We counted the number of new adults, using the method described above, each week.

Statistical analyses

Because the experimental design differed slightly between 2000 and 2001, we analyzed data from the two experiments separately. If plants died during the experiment or if plants never had more than 10 nymphs, they were excluded from analyses. Total sample size in 2000 was 136 and in 2001 it was 135.

The effects of host plant species and ant treatment on nymph number were analyzed with MANOVA. Dependent variables were the number of nymphs per plant on July 17 and July 29 in 2000 and the number of nymphs per plant on July 10 and July 23 in 2001. We added '1' to all datapoints and log transformed the number of nymphs per plant to normalize residuals to better meet the assumptions of MANOVA. We did not include data from the first survey in each year because ant manipulations had just been initiated and were unlikely to have had an effect. We did not include data from later surveys because nymphs had begun developing into adults and many plants had zero nymphs; data did not meet assumptions of MANOVA.

We tested the effects of host plant species and ant treatment on the total number of new adults (a cumulative measure of survival over the summer) with a combination of two-way ANOVA and a randomization program in True Basic™. Because a large proportion of the data were zeroes, no transformations changed the distribution of the residuals to meet assumptions of normality. Therefore, we could not assign significance to F values using an F distribution.

Instead, we used a randomization test to assign significance to calculated F values (Sokal and Rohlf, 1995). The distribution used to assign significance to F values was created from 1000 random mixings of the data.

Results

Both host plant species and presence of ants affected nymph number (Figs. 1 and 2). In July of 2000 and 2001 there were significantly more nymphs on *Wyethia* spp. than on *C. viscidiflorus*. The presence of ants increased nymph

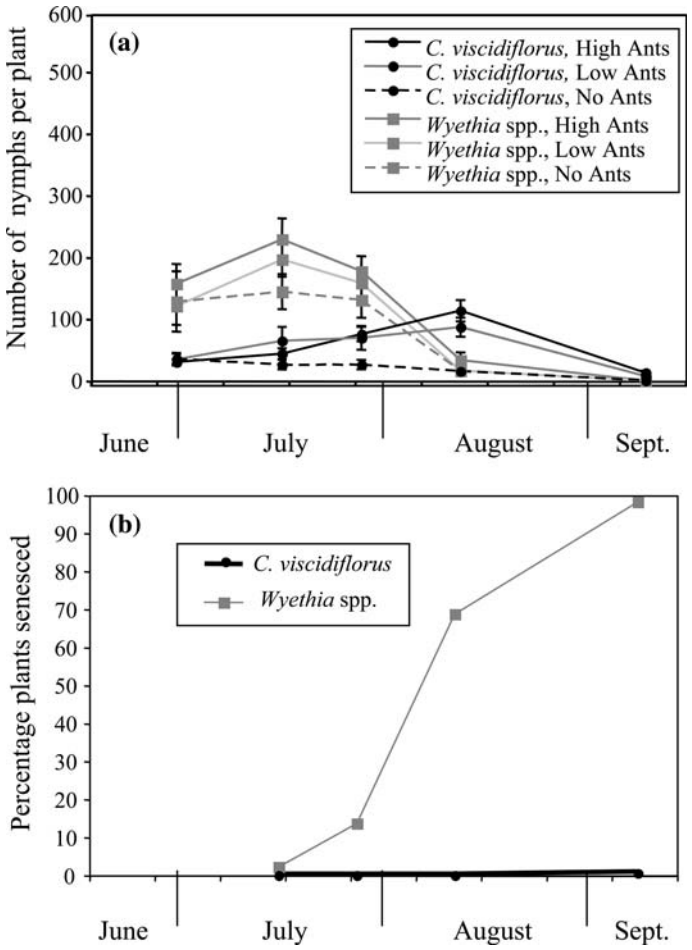

Figure 1. (a) Mean number of nymphs/plant over time in 2000 ($N = 136$). Error bars are ± 1 SE. There was a strong plant effect ($F_{2,129} = 56.54$, $p = 0.0001$) and an ant effect ($F_{4,258} = 4.08$, $p = 0.0032$), but no interaction effect ($F_{4,258} = 1.73$, $p = 0.14$) on nymph numbers (F-values based on Wilks' Lambda test statistics). Data for MANOVA were nymph numbers on July 17 and 29 in 2000. (b) Percentage of senesced plants over time in 2000.

number in 2000, but the effect of ants on nymph number in 2001 was only marginally significant. In neither year was there an interaction between the host plant and the ant treatments on nymph number in July.

In both 2000 and 2001, the effect of ants on the number of new adults depended on the host plant (Fig. 3); the presence of ants increased the number of new adults on *C. viscidiflourus* but had no significant effect on the number of new adults on *Wyethia* spp.

Using the absolute number of new adults as the dependent variable was more conservative than calculating the percentage of eggs surviving to adulthood. Because of a strong preference of ovipositing membracids for *Wyethia* spp.

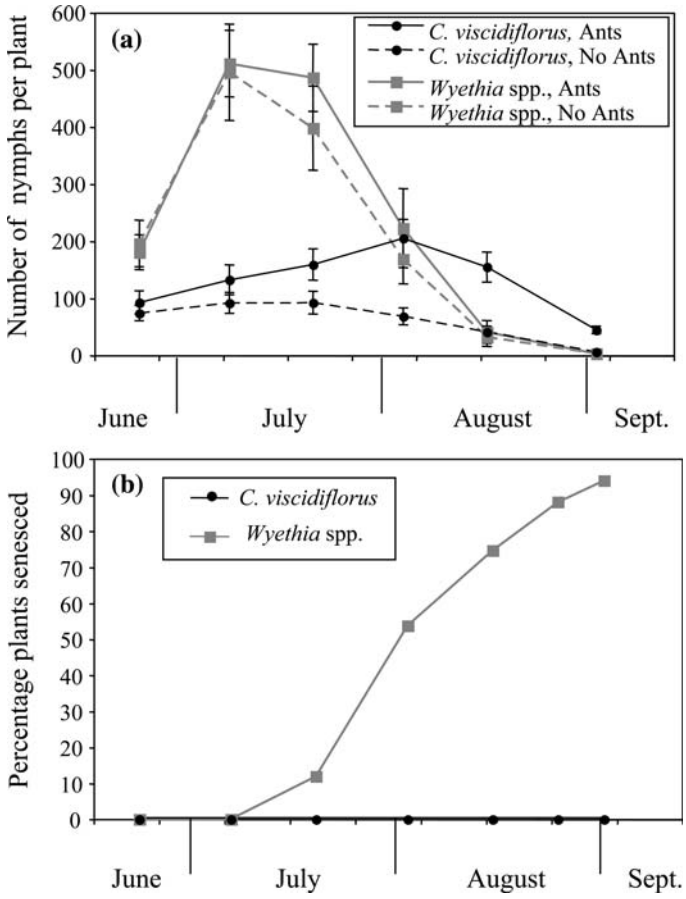

Figure 2. (a) Mean number of nymphs/plant over time in 2001 ($N = 135$). Error bars are ± 1 SE. There was a strong plant effect ($F_{2,130} = 39.41$, $p = 0.0001$), a marginal ant effect ($F_{2,130} = 2.83$, $p = 0.06$) and no interaction effect ($F_{2,130} = 1.44$, $p = 0.24$) on nymph numbers (F-values based on Wilks' Lambda test statistics) The degrees of freedom are different between years because the number of ant treatments differ. Data for MANOVA were nymph numbers on July 10 and 23 in 2001. (b) Percentage of senesced plants over time in 2001.

(Reithel, 2003), initial egg number on *Wyethia* spp. was greater than on *C. viscidiflorus* resulting in many more nymphs on *Wyethia* spp. than *C. viscidiflorus* (Figs.1 and 2). Even though initial egg number was higher on *Wyethia* spp., however, many more new adults developed on *C. viscidiflorus*. This difference between plants in membracid survival would have been even greater if we had used the percentage eggs surviving to adults as the dependent variable.

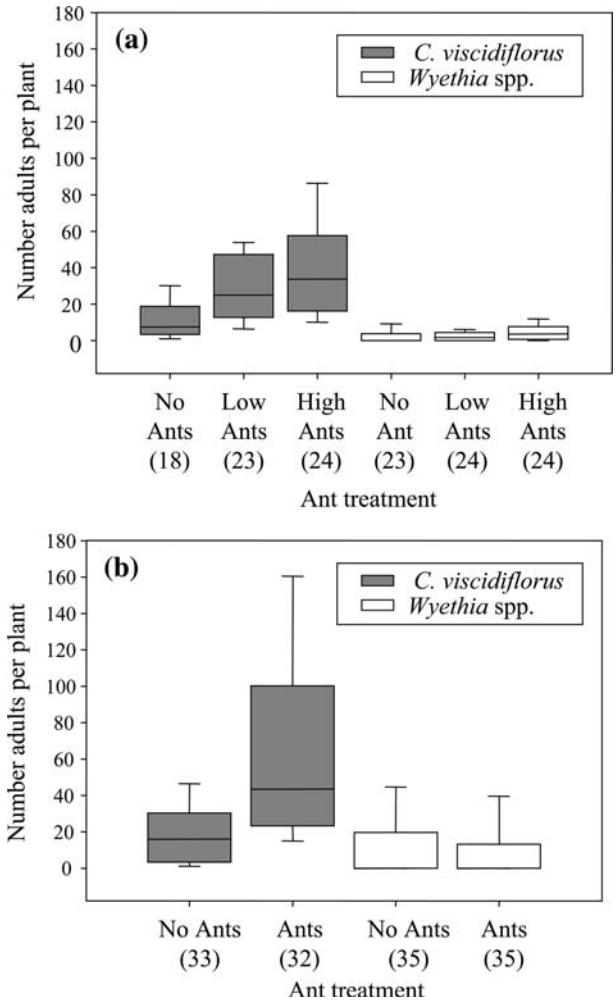

Figure 3. Effect of ant treatments on number of nymphs emerging into adults on a per plant basis in (a) 2000 and (b) 2001. Because data are strongly nonnormal, boxes show 25th and 75th percentiles and horizontal lines in boxes are median values. When boxes have no horizontal lines, medians are equal to zero. Bars represent 10th and 90th percentiles. Host plant species had a strong effect on new adult production in both 2000 and 2001 ($F_{1,130} = 31.34$, $p < 0.001$ and $F_{1,131} = 18.49$, $p < 0.001$, respectively) as did the presence of ants ($F_{1,130} = 2.94$, $p = 0.001$ and $F_{1,131} = 10.00$, $p < 0.001$) and the host plant × ant interaction ($F_{1,130} = 2.98$, $p < 0.001$ and $F_{1,131} = 14.14$, $p < 0.001$). See the methods for how *p*-values were calculated.

Wyethia spp. senesced earlier than *C. viscidiflorus* (Figs. 1 and 2); more than 60% of *Wyethia* spp. had senesced by mid-August in both years, whereas *C. viscidiflorus* did not begin to senesce until September. Furthermore, the date of *Wyethia* spp. senescence in 2001 was correlated with the number of new adults on *Wyethia* spp. ($\rho = 0.755$, $p = 0.0001$); more new adults emerged on plants that senesced later in the summer. In contrast, all new adults emerged on *C. viscidiflorus* before the plants senesced.

Discussion

The effect of ants on the membracids depended upon the host plant species. Ants had a positive effect on nymph number, regardless of the host species. However, this positive effect on nymph number did not translate into more adults on both host plant species. Ants increased the number of new adults on *C. viscidiflorus*, but not on *Wyethia* spp. Because the total number of new adults is a more complete measure of fitness than short-term estimates of nymph numbers, the ant–membracid interaction was a mutualism when membracids fed on *C. viscidiflorus* and a commensalism when membracids fed on *Wyethia* spp.

Patterns of host plant senescence were responsible for the absence of a mutualism on *Wyethia* spp. This host plant senesced in late July and August, causing huge mortality of nymphs (Figs. 1 and 2). Nymphs were third to fourth instars and either died on senescing *Wyethia* spp. or died as they attempted to move to new host plants. In contrast, nymphs on *C. viscidiflorus* developed into adults long before *C. viscidiflorus* senesced.

While nymphs have the potential to move off a host plant to avoid senescence, such movement is not sufficient to mitigate the effects of senescence of *Wyethia* spp. Experimental work indicates that under the best of circumstances, e.g., *C. viscidiflorus* is located within a quarter meter of senescing *Wyethia* spp., only 8% of nymphs successfully move to *C. viscidiflorus* from *Wyethia* spp. (Reithel, 2003). Consequently very few of the nymphs are able to successfully transfer off of senescing plants. Additionally, large aggregations of nymphs cause *Wyethia* spp. to senesce up to 5–10 days earlier (unpublished data). Any positive effect of ants on nymph survivorship would indirectly accelerate plant senescence, requiring nymphs to transfer between plants at smaller, more vulnerable instars. Therefore, any positive effect of ants on nymphs developing on *Wyethia* spp. is washed out by the large mortality associated with host plant senescence.

Wyethia spp. is an important host species at the Almont Triangle. At this site Reithel (2003) demonstrated that female membracids strongly prefer ovipositing on *Wyethia* spp. over *C. viscidiflorus*, despite poor performance on

Wyethia spp. Because females prefer to oviposit on *Wyethia* spp., *Wyethia* spp. is one of the most common host plants, representing 23% of the host plants used at this site. Interestingly, one of the other common host plants, *B. sagittata*, senesces even earlier than *Wyethia* spp. Therefore, over 50% of the host plants at the site senesce early enough that the beneficial effects of ants on nymphs cannot translate into more adults (Reithel, 2003).

The impact of host plant species on the mutualism was not an artifact of an unusual year or site. In all 3 years in which it was examined, *Wyethia* spp. was the inferior host plant at the Almont Triangle (Reithel, 2003). Furthermore, studies on oviposition preference and larval performance at an additional site indicate that *P. modesta* consistently makes poor choices, even when a different suite of host plants are present (Reithel, 2003). Consequently, the generalist lifestyle combined with a consistent pattern of poor decision-making concerning host plants undoubtedly creates significant variability in the outcome of the mutualism across the range of *P. modesta*.

These results, at least superficially, might be taken to indicate that insect generalists should be less likely to be engaged in mutualisms. It is not at all unusual for generalist insect herbivores to have a preference for host plants on which they perform poorly (e.g., Chew, 1977; Courtney, 1981; Thompson, 1988; review in Mayhew, 1997). Because maldaptive preferences would reduce or eliminate much of the benefits of ant-tending, generalist insects might be less likely to be involved in mutualisms, and/or are less likely to invest substantial resources in mutualisms. Paradoxically, in both membracids (Wood, 1984) and lycaenids (Pierce and Elgar, 1985) there is a positive association between being a generalist and engaging in ant mutualisms, suggesting that being a generalist herbivore is not a serious constraint to being involved in a mutualism.

The ecology of this mutualism suggests that the conditionality of the outcome does not necessarily reduce selection for investment by membracids in the mutualism. Membracids move on the order of meters (Reithel, 2003, pers. obs.) while host plants of different species are only centimeters apart. Additionally, there is no genetic differentiation associated with host plants (Reithel, 2003). Consequently, membracids freely mix among the different host plant species within populations. Rough estimates in a site with only *Wyethia* spp. and *C. viscidiflorus* plants (no *B. saggitatta*) suggest that approximately 90% of the new adults produced originate from *C. viscidiflorus* plants (pers. obs.); most new adults are being produced in an environment in which there is a considerable advantage to being ant-tended. For this reason, the lack of a positive effect of ants on membracids growing on *Wyethia* spp. should have only a limited effect on the evolution of the mutualism. This study makes it clear that the extent to which variable outcomes affect the evolutionary trajectory of the mutualism will depend upon the details of the system.

There is a growing body of research indicating that interactions between pairs of species depend upon the larger community context. Initial work on interaction modifications, or higher order interactions, focused on predator–prey relations (Billick and Case, 1994). Work on conditional outcomes in mutualisms has demonstrated the importance of predators to mediating mutualisms (Cushman and Whitham, 1989; Del-Claro and Oliveira, 2000). The results of this study suggest that the outcome of a mutualism can be significantly altered by a species not directly involved with the mutualism, in this case a bottom-up factor, and highlight the importance of investigating multiple ecological factors shaping species interactions. Understanding the ecological factors that shape where a particular interaction falls on the continuum from loose to tight mutualisms will require an understanding of the broad ecological context within which the interaction occurs.

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