

## Ecological Effects of Ant-aphid Mutualism on the Invasive Potential of *Foeniculum vulgare* in Northern California Coastal Scrub

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**Abstract** Mutualisms, interactions between species whereby both benefit, can alter ecosystems by affecting community structure and species' distributions. Aphid tending behavior by ants, a common mutualism, directly affects aphid population growth and distribution. Aphids consume plant phloem and excrete honeydew that is eaten by ants. In return, ants provide protection for aphids. *Foeniculum vulgare* is an invasive plant in coastal scrub habitats of California that hosts a mutualism between invasive Argentine ants (*Linepithema humile*) and three aphid species (*Cavariella aegipodii*, *Dysaphis apiifolia*, *Dysaphis foeniculus*). This association can modify insect assemblage and affect host plant distribution by impacting herbivory rates. Host plants may experience a net reduction in herbivory caused by release from insects like the native specialist lepidopteran, *Papilio zelicaon*. This may facilitate the invasive success of *F. vulgare*. In this study, I quantified the effects of the ant-aphid association on host plant growth and insect assemblage. I tracked growth of *F. vulgare* on ant-aphid hosts versus non-hosts and found no effect of aphid presence. I recorded the presence of other fauna and found significant reductions on plants hosting the mutualism. I also quantified an effect of the mutualists on the distribution of *P. zelicaon*. In a greenhouse experiment, I found that *P. zelicaon* reduced growth of *F. vulgare* while aphids did not. I conclude that the mutualism can increase plant fitness and may be an important factor in facilitating/maintaining the invasion of *F. vulgare*. There may be implications for *P. zelicaon* given the increasing prevalence of *L. humile*.

## Introduction

A mutualism is an obligate or facultative association between different species that is beneficial to each (Way 1963). In many ecosystems, mutualistic interactions maintain natural diversity and affect plant distribution and community structure (Christian 2001). Mutualisms can function in pollination, seed dispersal, resource acquisition and protection from predators. There is increasing evidence that these mutualistic associations help shape natural communities (Boucher 1982, Christian 2001, Richardson et al. 2000). Tending behavior by ants is one such mutualism that can have major implications for arthropod assemblages and plant distributions by excluding organisms from certain plants (Crutsinger et al. 2005, Cushman 1991, Floate and Whitham 1994). Many different species of ants have been observed tending homopterans (e.g. plant hoppers, aphids) and lepidopterans (moths and butterflies) in temperate and tropical regions around the world (Boucher 1982, Cushman 1991, Stadler and Dixon 2005, Way 1963). In ant-homopteran associations, ants provide aphids with protection from predators, parasitoids and fungal attack in return for the aphids' defecated, carbon-rich honeydew (Del-Claro and Oliveira 1993, Fischer and Shingleton 2001, Flatt and Weisser 2000).

There are a number of ecological effects associated with ant-aphid mutualism, including direct effects on aphid life history. For instance, ant tending positively contributes to aphid population growth, fecundity, developmental rates, and feeding rates (Breton and Addicott 1992a, Flatt and Weisser 2000). Furthermore, selective pressure on aphids may be influenced by competition for tending ants among aphid populations (Breton and Addicott 1992b, Fischer et al. 2001, Franks et al. 2004). Ant selectivity leads to adaptive challenges for aphids as they attempt to attract ants by associating with higher quality host plants and excreting more nutritious honeydew (Breton and Addicott 1992b, Cushman 1991). Ants also cause variation in herbivory and insect assemblage by increasing aphid populations and through their aggressive behavior toward other potential herbivores (Cushman and Addicott 1989, Del-Claro and Oliveira 1993, Fischer and Shingleton 2001). A review by Way (1963) documents many cases of ants' aggressive behavior towards other insects in the presence of a food source like aphids. As a result, tending behavior could give a selective advantage to certain host plant species based on their usefulness to aphids (Franks et al. 2004). Host plant selectivity is an important component of tending behavior by Argentine ants (*Linepithema humile*), which associate with three species of aphids (*Cavariella aegipodii*, *Dysaphis apiifolia*, *Dysaphis foeniculus*) in coastal scrub of the

East San Francisco Bay Area (Abraham, *Pers. Comm.*, Shors, *Pers. Comm.*). *D. apiifolia* is the only one of these species previously known to be tended by ants (Mills, *Pers. Comm.*). In this system, *L. humile* and the aforementioned aphid species commonly occur on sweet fennel (*Foeniculum vulgare*).

The interaction between *L. humile* and aphids may affect invasive success of *F. vulgare* by altering levels of herbivory by aphids and other organisms. Moreover, the literature demonstrates the potential of tending behavior to alter insect assemblage and herbivory patterns on host plant species (Cushman and Addicott 1989, Del-Claro and Oliveira 1993, Floate and Whitham 1994). While the host plant mediates the ant-aphid interaction, its distribution and phenology also affect its usefulness to the mutualists. For instance, *L. humile* populations are largest and most active in the spring and summer, the growth and flowering season of *F. vulgare* (Heller and Gordon 2006, Abraham, *pers. comm.*). Furthermore, *F. vulgare* is distributed widely in areas where *L. humile* and aphids are abundant (C. Dibble, *pers. obs.*). Thus, some hosts are inherently of higher quality to the mutualists, where host plant quality is defined not just by nutritional value, but also plant distribution and phenology relative to that of ants and aphids as well as physical plant characteristics, which may provide refuge and further protection for the symbionts. *F. vulgare* appears to be a suitable host given these criteria. Previous research in other systems has demonstrated that tending behavior can affect host plant fitness, but this question becomes particularly important in this system given the invasive success of *F. vulgare* may be facilitated by the ant-aphid interaction.

*F. vulgare* is an introduced perennial herb from Mediterranean Europe. It invades grasslands, coastal scrub, savannas, and banks of creeks, estuaries and bays (Brenton and Klinger 2002). Invasive success of introduced species like *F. vulgare* can be determined by a variety of factors including exposure to novel herbivores, mutualists and predators (Mitchell et al. 2006), release from those in their native range (Keane and Crawley 2002) and altered allelopathic effects (Ridenour and Callaway 2001). Invasive plants can alter fire regimes, nutrient cycling, hydrology, and energy distribution in ecosystems, potentially devastating native species (D'Antonio and Vitousek 1992, Mack et al. 2000). On Santa Cruz Island, California, *F. vulgare* reduced native plant species richness and diversity (Ogden and Rejmanek 2005). Plant demography was affected so drastically that native populations did not recover even after the

invader was controlled. The present study asks whether the ecological consequences of ant-aphid mutualism are important to the invasive success of *F. vulgare*.

Overall, I sought to determine if the effects of tending behavior on insect assemblage are significant in this system and whether they may contribute to the invasive dominance of *F. vulgare*. With a combination of approaches, I tested the general hypothesis that ant-aphid presence confers a fitness advantage to host plants by reducing net herbivory through the exclusion of herbivores like the native anise swallowtail caterpillar *Papilio zelicaon*.

Using field surveys, I asked the following questions: 1) How prevalent is tending behavior on *F. vulgare* in coastal scrub ecosystems in Northern California and is tending more common on plants of a particular size? 2) To what degree do ant-aphid interactions alter insect assemblage on *F. vulgare*? 3) Is growth of *F. vulgare* affected by aphid presence? 4) How does tending behavior affect the distribution of *P. zelicaon*? My hypotheses were: 1) Tending behavior is widespread and varies with host plant size. 2) Insect abundance and richness decrease in the presence of tending *L. humile*. 3) *F. vulgare* individuals that host aphids and *L. humile* do not experience significant reductions in growth (similar results have been shown in the literature; see Discussion). 4) *P. zelicaon* larvae are distributed farther from ant-aphid host plants than non-host plants.

I chose to look specifically at *P. zelicaon* because, as a specialist, it has the potential to cause significant damage to *F. vulgare* and its phenology is closely tied to that of its host plant so alterations in either of their distributions might lead to population reductions for the native caterpillar. Two other plant species, water hemlock (*Cicuta spp.*) and water dropwort (*Oenanthe spp.*), both natives, are the only other hosts that could sustain the breeding of *P. zelicaon* in the summer in its low elevation range in Northern California (Tong and Shapiro 1989). Neither of these species is found in this study system, so *P. zelicaon* relies on the invader. This situation arose through an evolutionary host shift, whereby the introduction of a suitable host species causes the relatively rapid specialization of a native species (Thompson 1993). *P. zelicaon* adults choose to deposit their eggs on particular plants (Wehling and Thompson 1997) and, in this case, favor *F. vulgare*. Once eggs are laid, the larvae are relatively immobile. Thus, tending behavior may affect oviposition selectivity and lead to alterations in the distribution of *P. zelicaon* larvae.

I also used a greenhouse experiment to determine the relative effects of aphid herbivory versus that of *P. zelicaon*. I used aphids in the *Dysaphis* genus for my greenhouse study because

they were more commonly tended in the field. I tested the hypothesis that *P. zelicaon* herbivory will significantly reduce growth of *F. vulgare* while that of *Dysaphis spp.* will not. This question is relevant only if the ant-aphid mutualists cause a change in the distribution of *P. zelicaon*, as this would imply any difference in herbivory between aphids and *P. zelicaon* could affect invasive success of *F. vulgare*. Even if that were not the case, my greenhouse experiment helped to determine the effects of *Dysaphis spp.* herbivory in a controlled setting.

Previous studies have quantified ecological variation resulting from ant-aphid interactions, but few have sought to correlate this variation with invasive success of an exotic species. Ant-aphid mutualism is particularly important in this system because *P. zelicaon*, whose larvae rely on *F. vulgare*, is a native species and has the potential to interact closely with the invasive ants. A release from *P. zelicaon* herbivory by ant-aphid mutualists could facilitate the invasive dominance of *F. vulgare* and conservation issues for the native lepidopteran may arise as *L. humile* spreads. Given what is known about the potentially overwhelming effects of exotic plants (Brenton and Klinger 2002, D'antonio and Vitousek 1992) and the role mutualisms can play in invasions (Christian 2001, Richardson et al. 2000), it is critical to gain more knowledge about the mechanisms through which biotic interactions can affect invasive potential and plant fitness.

## Methods

**Field Work** I collected all field survey data from April to September of 2008 at the Albany Bulb and Point Isabella East Bay Regional Parks. Each site had two 20 m transects (Fig. 1a, b) where I chose plants at approximate one meter intervals ( $n = 20$  for transects A, B and C,  $n = 18$  for transect D). Random sampling was impractical given the patchy distribution of *F. vulgare*. I chose the location of each transect based on the abundance of *F. vulgare* so that I could track evenly spaced plants. All transects had *F. vulgare* at  $< 1$  m intervals that were not included. I tagged and numbered each plant and collected data on a weekly basis. In the field I tracked: 1) plant height 2) number of aphids 3) number of ants 4) number of individuals other than ants and aphids 5) number of species other than ants and aphids. I specifically noted the presence or absence of *P. zelicaon* as well.

To address the question of whether ants affect the distribution of *P. zelicaon*, I created a 15 by 35 meter plot at the Albany Bulb, approximately 30 m West of transect A. I noted each

plant's ant-aphid host status ( $n = 106$  plants), presence/absence of *P. zelicaton* larvae and the distance to the nearest plant with ants present. For plants hosting ants, this latter value was zero.



Figure 1 (a) Field survey site 1 at the Albany Bulb, Albany, CA. Transects A ( $n = 20$ ) and B ( $n = 20$ ) were monitored here, each 20 m long. (b) Field survey site 2 at Point Isabella, Richmond, CA. Transects C ( $n = 20$ ) and D ( $n = 18$ ) were monitored here, each 20 m long.

**Statistical Analysis of Field Data** I performed a chi-squared analysis of a 4x4 matrix of ant and aphid densities to test for a positive correlation between the two mutualists. This was aimed at understanding how common tending behavior was in the field. Aphid densities were 0 (absent), low (1-20), medium (21-50) and high (>50). Ant densities were 0 (absent), low (1-4), medium (5-8) and high (>8). I chose these categorical values based on the range of each species observed in the field.

To determine the effect of tending behavior on insect assemblage, I compared mean richness and mean abundance of taxa other than ants and aphids on host plants versus non-host plants using one-way ANOVA. Richness was defined as the total number of other species present while abundance was the total number of other individuals present on a given plant. These measures allowed me to quantify the assemblage on *F. vulgare* and determine if ant-aphid presence excludes other organisms.

I compared the mean heights of hosts versus non-hosts to test whether the mutualists showed a preference for plants of a particular size. This analysis was done using one-way ANOVA as well.

I used relative growth rates (RGR) for field work analysis to account for variation in the initial heights of *F. vulgare* individuals. I measured for a difference in the mean RGR of *F. vulgare* hosts versus non-hosts using one-way ANOVA. I calculated RGR using the equation:

$$RGR = \frac{[\ln(\text{height}_2) - \ln(\text{height}_1)]}{\text{time}_2 - \text{time}_1}$$

where  $\text{height}_2$  was the final height, recorded at  $\text{time}_2$ , and  $\text{height}_1$  was the initial height, recorded at  $\text{time}_1$ . I ran this ANOVA using two different definitions for ant-aphid host plant: the mutualists were present for at least one sampling date and the mutualists were present for at least half of the sampling dates. I also tested for an effect of aphids on RGR by using linear regression of the proportion of sampling dates as a host versus RGR. For the regression analysis, I only considered a plant a host if it had at least medium aphid density (21-50 individuals). This allowed me to be certain that the aphids had not recently established on the plant, which would significantly reduce the chance that they had caused a measurable decrease in RGR.

I employed logistic regression to determine if the distance from ant-aphid host plants had a significant effect on *P. zelicaon* distribution. I never observed larvae moving to different individual plants than that on which they were born, so I expected this analysis to accurately depict an alteration in their distribution with respect to ant-aphid hosts.

**Greenhouse Experiment** I also conducted greenhouse work in the summer of 2008 at the Berkeley Oxford Tract Lath houses. I manipulated insects in three treatments: 1) no insects (control,  $n = 8$ ) 2) aphids ( $n = 11$ ) 3) *P. zelicaon* larvae ( $n = 8$ ). Persistent problems with ant colony survival in the greenhouse caused me to terminate a fourth treatment with ants and aphids. For this reason, the aphid treatment began with 20 replicates, but only 11 were used in the analysis because aphids failed to establish on the other nine. Aphid presence alone remains useful in isolating the relative effects of herbivory on *F. vulgare*, which was ultimately the goal of this experiment. All plants were grown from seeds that came from the same parent plant and were collected by Joel Abraham in 2004. On 5 May 2008, after germination, I transferred seedlings to 15 cm cone containers with organic potting soil where they remained for the rest of the experiment. I introduced insects to the plants on 5 July 2008 when the plants were well established. Plants were watered daily and given nutrients three days a week (liquid fertilizer mixed in with watering). Insects were controlled with greenhouse tents each housing four or five plants distributed in a 20-space (four by five) rack. Insects within each tent were free to move

among those four or five plants. For these treatments, I monitored aphid population growth and plant growth. I collected aphids from the field and introduced them at low density, between three and six individuals per plant. I used *P. zelicaon* larvae collected in the field for greenhouse work and placed one caterpillar on each plant initially. All *P. zelicaon* larvae were first or second instar except for one third instar, which was included for a lack of younger individuals (*P. zelicaon* has five larval instar stages in its lifecycle).

**Statistical Analysis of Greenhouse Data** I first tested for a difference in initial height of the greenhouse plants using one-way ANOVA to justify the use of absolute growth rate (AGR) instead of RGR, which was necessary because one plant in the *P. zelicaon* treatment was killed by herbivory before the second sampling date. I calculated AGR as:

$$AGR = \frac{height_2 - height_1}{time_2 - time_1}$$

where  $height_2$  was the final height, recorded at  $time_2$ , and  $height_1$  was the initial height, recorded at  $time_1$ . I compared mean AGR of control plants versus the two insect treatments using one-way ANOVA and post hoc hypothesis testing with Tukey tests. This analysis tested the hypothesis that AGR would be greater on control plants than the insect treatments and that *P. zelicaon* would cause more damage than *Dysaphis spp.* All statistical analyses were conducted using Systat 11 (Cranes Software International, Bangalore, India).

## Results

**Field Work** I found a positive, non-random association between ants and aphids in this system ( $\chi^2 = 323.07$ ,  $df = 327$ ,  $p < .001$ ). The largest deviations from the expected distribution occurred when ants and aphids were both absent and when they were both at high densities indicating that aphids were rarely found untended and more ants were typically found tending at higher aphid densities (Fig. 2). Of 277 total *F. vulgare* samples, 43% hosted the ant-aphid mutualism and of 170 samples that had aphids, 87.6% also had ants.

The ant-aphid interaction appears to exclude other organisms (insects and gastropods) from host plants. Overall, there was a 26.3% reduction in species richness (ANOVA,  $F = 3.866$ ,  $df = 327$ ,  $p = 0.05$ ) and a 23.3% reduction in species abundance (ANOVA,  $F = 4.144$ ,  $df = 327$ ,  $p = 0.043$ ) in the presence of tending behavior (Fig. 3). Furthermore, I found that plants hosting *P.*



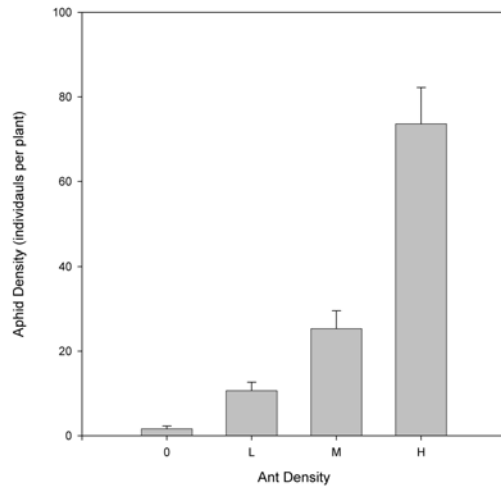


Figure 2. *L. humile* and aphid densities were significantly correlated on *F. vulgare* in the field ( $\chi^2 = 323.07$ ,  $df = 327$ ,  $p < .001$ ) indicating the prevalence of this mutualism in East San Francisco Bay. Per plant ant densities were: 0 = absent, L = 1-4, M = 5-8, H > 8. These categorical values were based on observations during the field surveys.

*zelicaon* larvae were distributed an average of 147 cm from ant-aphid host plants compared to 62.9 cm for controls, an 80.1% difference (Logistic Regression,  $F = 3.932$ ,  $df = 105$ ,  $p = 0.047$ ).

Plants that hosted aphids were 24.2% shorter in the field than those without aphids (ANOVA,  $F = 6.665$ ,  $df = 325$ ,  $p = .01$ ). RGR was not affected by the host status of *F. vulgare* when hosts had ants and aphids for at least one sampling date (ANOVA,  $F_{1,72}$

$= 0.469$ ,  $p = 0.495$ ) nor when hosts had ants and aphids for at least half of the sampling dates (ANOVA,  $F_{1,72} = 0.202$ ,  $p = 0.654$ ). Furthermore,

aphid presence did not affect RGR of *F. vulgare* when measured as the proportion of surveys with aphids present (Linear Regression,  $F = 2.530$ ,  $df =$

72,  $p = 0.116$ ). Eight samples included in this

regression had negative RGR over the course of the study and, of those, six hosted aphids for less than half of the sample dates. Nevertheless, the a posteriori hypothesis that RGR was more likely to be negative for plants that hosted aphids for fewer than 50% of the sample dates was not supported ( $\chi^2 = 2.0$ ,  $df = 7$ ,  $p = 0.157$ ).

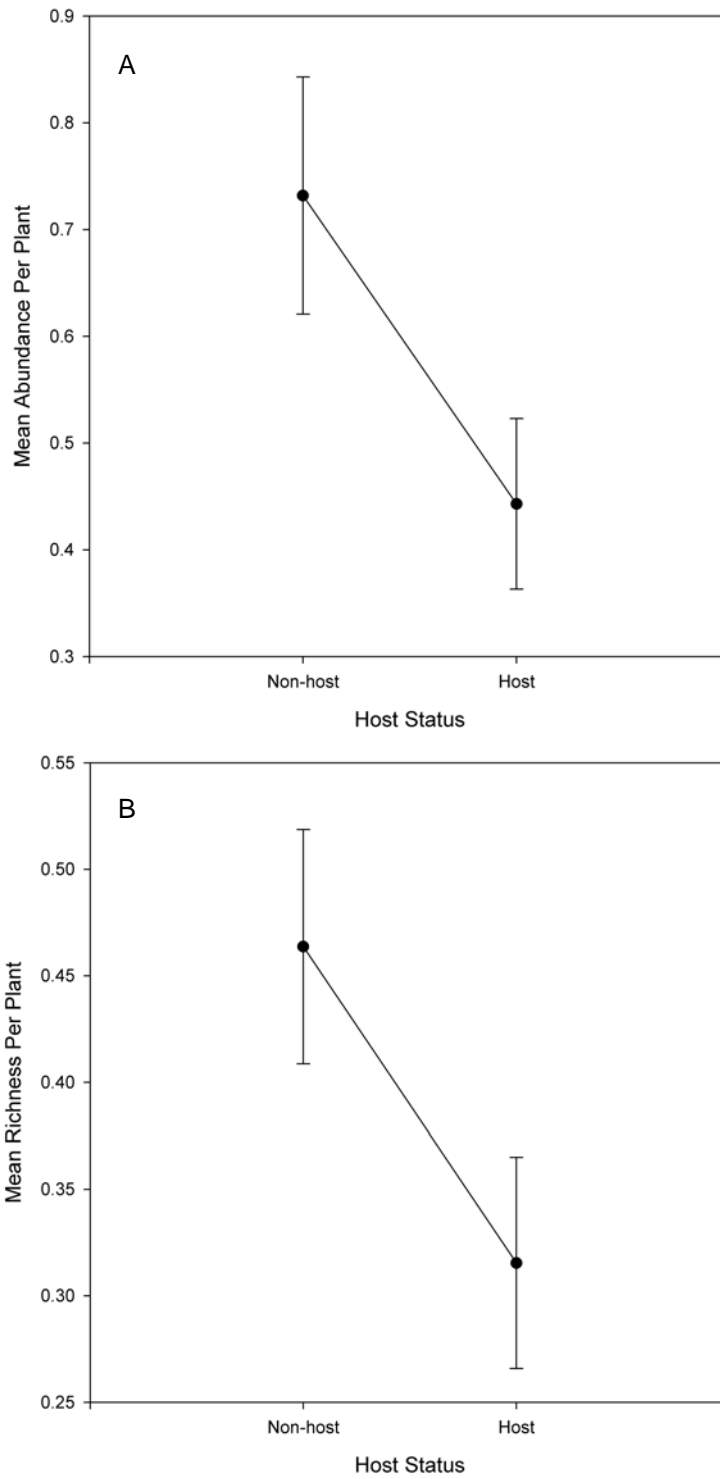


Figure 3. Reduction in species abundance (A) and richness (B) on ant-aphid host plants versus non-hosts.

**Greenhouse Experiment** The initial heights of greenhouse plants were not significantly different (ANOVA,  $F = 1.260$ ,  $p = 0.302$ ) so AGR is a representative measure of growth in the greenhouse. AGR of *F. vulgare* among the three greenhouse treatments was significantly different (ANOVA,  $F_{2, 24} = 4.741$ ,  $p = .018$ ). Plants in the *P. zelicaon* treatment had a negative mean AGR that was significantly lower than that of the control (Tukey tests,  $p = .038$ ) and aphid (Tukey tests,  $p = .028$ ) treatments (Fig. 4). Aphid treatment plants were not significantly different from controls (Tukey tests,  $p = .998$ ). Control and aphid treatment plants showed similar growth patterns while the change in average height of *P. zelicaon* host plants through time indicates the magnitude of the damage those plants received (Fig. 5). At the end of the greenhouse study, the average plant in the *P. zelicaon* treatment was 65.8% shorter than the average of the control and aphid treatments.

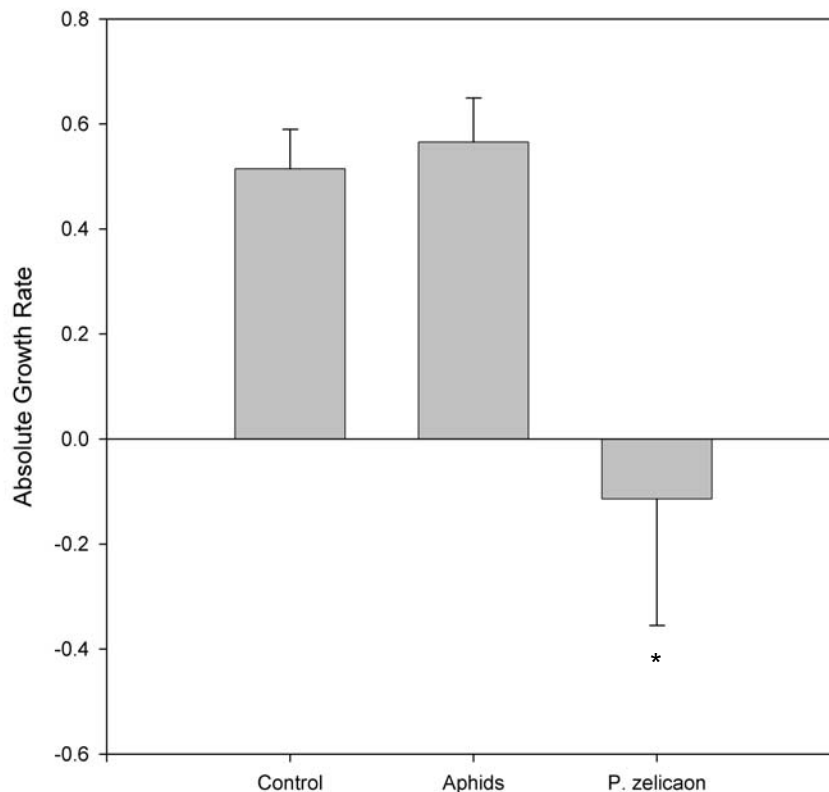


Figure 4. Mean absolute growth rates of *F. vulgare* in control, aphid and *P. zelicaon* treatments. Significant differences from the control are indicated by an asterisk.

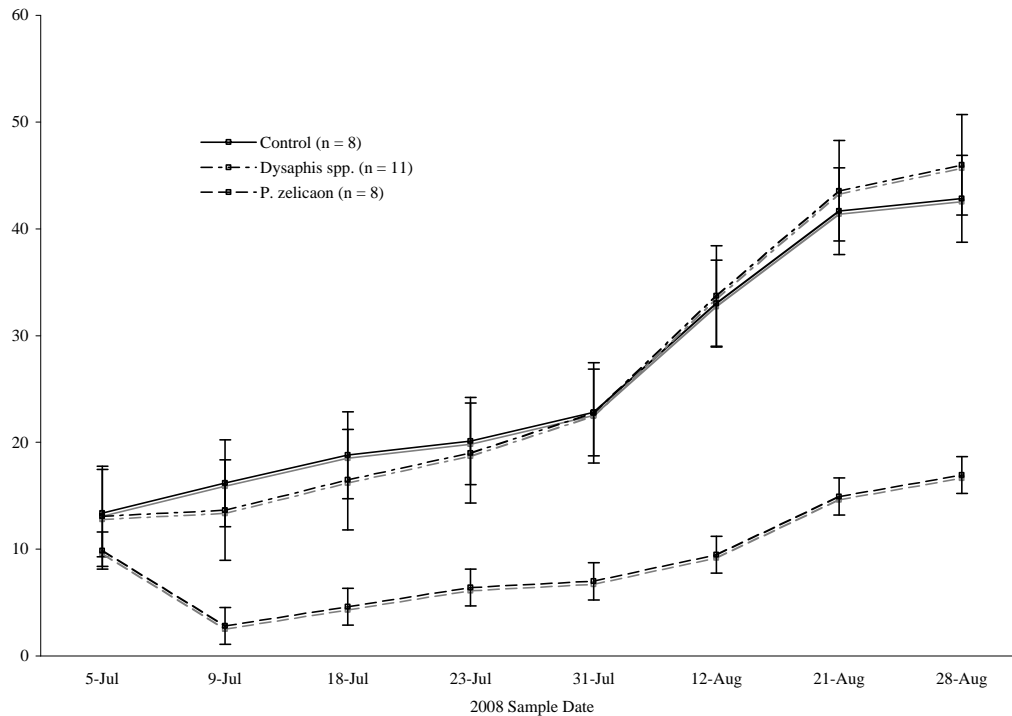


Figure 5. Average height of *F. vulgare* in three treatments over the course of the 2008 greenhouse study. All *P. zelicaon* died before the 23 July sample because they ate virtually all the plant material available. Some plants recovered though, which accounts for the increase seen in the *P. zelicaon* treatment thereafter.

## Discussion

I quantified the occurrence of the interaction between *L. humile* and *C. aegipodii*, *D. apiifolia* and *D. foeniculus*, indicating the broader ecological relevance of any effects of the mutualism. The field portion of this study illustrates the prevalence of the mutualism on *F. vulgare*. Although aphids were found in the absence of ants, these occurrences were relatively rare. Furthermore, major deviations from an expected random distribution of ants and aphids occurred for: low ants, low aphids; zero ants, zero aphids; and high ants, high aphids (in order of increasing chi-square value) indicating the correlation between their abundances and highlighting the importance of any ecosystem impacts. In a system where aphids occur in the presence of ants 87.6% of the time, any impacts of the interaction are likely to be quantifiable. These ecological effects include alterations in the insect community structure and impacts on host-plant growth.

Given reductions in both richness and abundance of species other than *L. humile* and aphids on host plants in the field, it is conceivable that *F. vulgare* hosts experience altered net herbivory

compared to non-hosts, which could affect fitness. A number of studies have quantified alterations in arthropod community structure due to ant-aphid presence where the association negatively affected a range of ecological guilds (Floate and Whitham 1993, Wimp and Whitham 2001). Ant presence can affect hunting behavior of other organisms (Halaj et al. 1997) and cause higher occupation of prey refugia (Crutsinger and Sanders 2005). In these cases, however, herbivory is increased by aphid presence and therefore the association is likely to impact the host plant in a negative way. In the present study, the impact of ant-aphid mutualism on host plant fitness is less obvious because the exclusion of various other herbivores may cause a net reduction in damage suffered by the host plant despite the increase in aphid abundance. The reductions in species richness and abundance in the presence of tending ants could help explain the invasive success of *F. vulgare* if the exclusion of other herbivores outweighs the impacts of aphid damage.

I found evidence in both field and greenhouse work that supports the hypothesis that the ant-aphid interaction confers a net benefit to *F. vulgare*. The first such result regards the effect of aphid herbivory on *F. vulgare*. If ant-aphid host plants experienced reduced growth, the negative impacts of the mutualism would have to outweigh the positive impacts of release from other herbivores. However, I found that the percentage of samples with ants and aphids, a measure of the status of a given *F. vulgare* individual as an ant-aphid host, had no significant effect on relative growth rates. In fact, 75% of plants that experienced negative RGR overall in the field hosted aphids for less than 40% of the study. Furthermore, *Dysaphis spp.* did not affect AGR in the greenhouse. These results could be explained in three ways: 1) aphid herbivory does not impact plant growth 2) non-host plants and/or plants that hosted aphids for a shorter duration of the study are attacked by other herbivores that are more detrimental 3) ants maintain aphid populations at densities that are low enough to mitigate their negative effects on host plants. These explanations are likely to be non-exclusive and may vary temporally or spatially. The results of growth rate analyses suggest that the lower mean height of ant-aphid host plants in the field represents a preference of the mutualists for shorter plants rather than a reduction in the height of host plants. This preference could be due to less wind disturbance, lower defensible area and more natural protection on shorter plants, whose stalks, where ants and aphids are usually found, tend to grow closer to the main stem. A posteriori reasoning aside, this result is important in the context of my greenhouse work, which showed that *P. zelicaon* herbivory can

quickly kill relatively short plants (although greenhouse plants were shorter than the average ant-aphid host in the field). In the *P. zelicaon* greenhouse treatment, all of the larvae died before the fourth sampling date because they had diminished their food source. Thus, the effects of the ant-aphid interaction may be amplified by excluding *P. zelicaon* from the more vulnerable *F. vulgare* individuals.

Several studies provide further evidence of the potential for ant-aphid host plants to experience a net reduction in herbivory. Crutsinger and Sanders (2005) found greater herbivory on willow tree branches that lacked aphid-ant interactions. Floate and Whitham (1993) found that, by reducing the abundance of a specialist beetle, ant-aphid presence reduced total herbivory on cottonwood trees. Skinner and Whittaker (1981) demonstrated an eightfold decrease in defoliation and a reduction in caterpillar presence on trees with tending. However, none of these studies involved introduced species. The results of the present study create a link between a plant invasion and similar alterations in herbivory. I demonstrated reduced growth of *F. vulgare* due to *P. zelicaon* herbivory in the greenhouse and that aphids did not significantly affect *F. vulgare* growth. Therefore, the fitness and invasive success of *F. vulgare* could be facilitated by the exclusion of the more damaging *P. zelicaon* larvae by the ant-aphid mutualism.

As a specialist herbivore, *P. zelicaon* has the potential to cause significant damage to *F. vulgare* in this system, so changes to its distribution are particularly relevant. Furthermore, *P. zelicaon* is important from a conservation standpoint due to its status as a California native in a system otherwise dominated by exotic and invasive species. A number of studies have shown that native herbivores can act as controls of introduced plants (e.g. Agrawal and Kotanen 2003 but see review by Maron and Vila 2001). In the present system, another invader, *L. humile*, may prevent the native *P. zelicaon* from controlling *F. vulgare*. I rarely found *P. zelicaon* on plants that hosted the ant-aphid mutualism in the field and my results show that its distribution, which is contingent upon oviposition selectivity in reproductive adults, is affected by ant-aphid presence. The exclusion of *P. zelicaon* demonstrates the net positive effects that can be experienced by *F. vulgare* individuals that host the mutualism and thus establishes a specific link between plant fitness and host status. There are many potential mechanisms driving any plant invasion, but this study identifies release from *P. zelicaon* herbivory as a component of *F. vulgare* success in this system. The magnitude of this facilitation likely depends on the prevalence of *P. zelicaon* on a larger scale. If its populations are sufficiently large, the herbivory

that results could be a significant check on the spread of *F. vulgare*. Likewise, if tending *L. humile* are sufficiently abundant, they may completely inhibit the ability of native herbivores to control *F. vulgare*.

The spatial extent of the effects associated with ant-aphid mutualism remains unclear and may provide key insight into the potential for the association to facilitate the spread of *F. vulgare*. One study found that aphid abundance declined by 88% on host plants six meters or further from an ant nest because of their dependence on the association with ants (Wimp and Whitham 2001). This decline in aphid abundance and tending behavior begets changes in community structure and herbivory as corroborated by the present study. Thus it is important to consider the abundance and spatial extent of the ant-aphid mutualism in order to understand how it may increase the success of *F. vulgare* on larger scales. Similarly, the abundance and distribution of *P. zelicaon* is critical to understanding its ability to inhibit the success of *F. vulgare*.

To summarize, this study demonstrated the ecological effects of ant-aphid mutualism on insect assemblage and relative growth rates of ant-aphid hosts and non-hosts. This association plays a major role in determining community composition. Furthermore, it may have implications for the distribution of a native caterpillar, *P. zelicaon*, which could raise conservation issues if ant-aphid prevalence reduces its viable habitat. Both field and greenhouse work provide evidence that ant-aphid mutualism should be considered a contributing factor to the invasive potential of *F. vulgare*. This is not necessarily due entirely to the exclusion of *P. zelicaon*, but it seems evident that the caterpillar plays a major role. Future work should focus on the breadth of the effect of ant-aphid mutualism on landscape scales and in habitats across the invasive ranges of *F. vulgare* and *L. humile*. The possible use of *P. zelicaon* for biological control of *F. vulgare* should also be investigated, though it is unlikely to be significantly effective in systems where the ant-aphid mutualism is common.

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