

THE RELATIVE IMPORTANCE OF SPATIAL VS. TEMPORAL VARIABILITY IN GENERATING A CONDITIONAL MUTUALISM

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Abstract. We explored the relative importance of temporal vs. spatial variability to the conditionality of a mutualism between the treehopper *Publilia modesta* and the ant *Formica obscuripes*. The effect of the ants on the membracids varied considerably among years. When the effect of the ants on the membracids was estimated in five sites spread over 5 km there was mixed evidence for spatial conditionality in the mutualism. Using repeated surveys of nymph number we found that the effect of the ants on nymph number varied among sites through time. When total new adult production was examined, however, no such interaction between ants and location was evident. Aggregations displayed strong negative density-dependent adult production. Thus, while in some sites ants had a greater positive effect on nymph survivorship, aggregations at those sites produced proportionately fewer adults because of negative density dependence. Density dependence reduced or eliminated spatial differences in the effect of the ants on the membracids. Differences among sites did not explain spatial variation in the effect of ants on nymphs or new adult production. We conclude that temporal variability is much more important than spatial variability in generating conditionality in the mutualism.

Key words: ants; density dependence; *Formica obscuripes*; mutualism, conditional; *Publilia modesta*; spatial vs. temporal variability; treehoppers.

INTRODUCTION

Mutualisms fall within a continuum from loose to tight relationships (Margulis 1993). Loose relationships are facultative, may potentially involve individuals from a range of species, and may consist of only intermittent interactions. On the other end of the continuum, tight relationships are commonly obligative, involve individuals of specific species, and organisms may live in close contact. The ecological and evolutionary forces that determine where relationships fall on this continuum can shed light on mutualisms and cooperative behavior in general (Smith and Szathmari 1995).

Understanding the ecological forces shaping a mutualism requires insight into how a mutualism varies in space and time, a phenomenon termed a conditional mutualism (Herre et al. 1999). For example, an inability to consistently find partners will select for facultative mutualisms (Bronstein 1994), while consistently interacting with partners from a particular species may be a necessary precondition for the evolution of species-specific mutualisms (Horvitz and Schemske 1990, Wasser et al. 1996). Many mutualists invest energy in the relationship regardless of whether the partner is present or not (Stadler et al. 2001). Consequently, variability in the benefit received from the mutualism will affect

the investment a partner is willing to make in such a relationship. Ideally, studies of conditional mutualisms should document variation in aspects of the relationship, link that variation to the fitness of at least one of the partners, and identify the mechanism generating the variation.

Mutualisms involving ants tending insects and plants have been important model systems for studying mutualisms. There is strong evidence from ant-tended insects and plants that the nature of mutualisms can vary in time and space. The species of ants that tend insects and plants often varies spatially (Horvitz and Schemske 1990, Peterson 1995), and variation in tending patterns affects fitness (Addicott 1979, Messina 1981, Bristow 1984, Horvitz and Schemske 1984, Rico-Gray and Thien 1989, Wagner 1993, Fraser 1997). Offenberg (2001) demonstrated in an artificial setting that whether ants protect or prey upon their partners can depend upon availability of additional food resources. Additionally, aspects of the host plant upon which insects feed can affect levels of ant tending (Pierce and Eastel 1986, Fiedler 1990, Baylis and Pierce 1991), as can developmental stage of the insects being tended (Pierce and Eastel 1986, Peterson 1995, Billick et al. 2001). Not surprisingly, ant density has been related to variation in the strength of the mutualism (Bentley 1976, Barton 1986, Cushman and Addicott 1989, Breton and Addicott 1992, Morales 2000a).

Bronstein (1994) identified a study of an ant–treehopper mutualism by Cushman and Whitham (1989) as one of the few thoroughly documented instances of

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PLATE 1. *Publilia modesta* nymphs being tended by an ant worker (*Formica* spp.). The plant species is *Chrysothamnus viscidiflorus*. Photograph by Christopher Brown.

a conditional mutualism. In this interaction ants significantly increased survivorship of nymphs of *Publilia modesta* in two of three years. Salticid spider density was low in the year in which no ant effect was detected and variation in salticid numbers apparently generated variation in the effect of the ants on the membracids. Temporal variability is not the only possible source of variability in the relationship between treehoppers and ants, however; spatial variability may be just as important in generating conditionality in the mutualism. No study, however, has looked at the relative importance of spatial and temporal variability in an ant-tended mutualism.

We examined the role of both temporal and spatial variability in generating a conditional mutualism. Specifically, we repeated the experiment conducted by Cushman and Whitham (1989) in Arizona on *P. modesta* to determine whether such temporal variability could be detected at a site in Colorado over a period of three years. Additionally, we asked whether spatial variability in the strength of the ant–treehopper mutualism could also be detected by examining the effect of the ants on the membracids in five different sites spread over 5 km within a single year. By extending our experiments in both space and time we were able to estimate the relative importance of spatial vs. temporal dimensions to generating variability in the effect of the ants on the membracids. Additionally, in our spatial variation study we asked whether using a more complete measure of fitness, survivorship to adult, yielded different results than the traditional measure of short-term nymph survivorship. Finally, to identify the mechanism generating spatial variation in the mutu-

alism, we measured a number of site characteristics: the number of ants foraging at the different sites, the number of ants per nymph within aggregations, the relative number of spiders on plants at the different sites, and the phenology of the plants. We then tested whether these traits varied among sites and whether among-site variation in these traits explained spatial variation in the effect of the ants on the treehoppers.

METHODS

Study site and organism

This study was conducted in the Almont Triangle management area of the Gunnison National Forest ~25 km north of Gunnison, Colorado, USA. The site is relatively arid and the dominant plants are the woody perennials *Artemisia tridentata* and *Chrysothamnus viscidiflorus*. The remaining vegetation consists primarily of grasses and herbaceous perennials.

Publilia modesta occurs primarily in the western United States (Kopp and Yonke 1973). *Publilia modesta* nymphs aggregate, adult females stay with nymphs during development, and ants tend adults and nymphs (Kopp and Yonke 1973). Primary host plants at this site include *Chrysothamnus viscidiflorus* and *Wyethia* spp., which are both perennials in the Asteraceae family. Females oviposit in slits in the stems of plants in May and early June. Eggs hatch and nymphs emerge from plant stems from late June through early July. There is only one generation per year at this site. Nymphs feed on the host plant from which they emerged and do not leave their host unless the plant senesces (J. Reithel, *personal communication*).

Nymphs go through five instars and emerge into adults from mid-August through September. We estimate the time from first instar to adulthood to be 50–75 d. Adult females generally stay with nymphs at least until nymphs begin emerging into adults in August and possibly longer. We have observed nymphs in spider webs and coccinellid adults consuming nymphs.

A number of different ant species tend *P. modesta* throughout its range (see Plate 1). At the Almont Triangle the primary attendant is *Formica obscuripes*. Nest density is unusually high at this site with nearest neighbor distances on the order of a few meters. Ants visit the treehoppers to collect honeydew secretions. Ants benefit treehoppers by reducing predation by coccinellid larvae and salticid spiders (Cushman and Whitham 1989), though ants may also increase survivorship through waste removal (e.g., Morales 2000b).

Temporal variation experiment

In 1998, 1999, and 2001 we estimated the effect of the ants on the membracids at a single location in the Almont Triangle. In each of these years we set up the experiment in late June just as nymphs were first eclosing from eggs. We tagged between 30 and 80 *C. viscidiflorus* plants that had evidence of membracids; either nymphs or oviposition scars were present. We trimmed plants and placed duct tape on the base of the stem of each plant. Plants were randomly assigned to an ant removal treatment and a control treatment. We covered the duct tape in the ant exclusion treatment with Tanglefoot (Tanglefoot Company, Grand Rapids, Michigan, USA) and removed all vegetation touching or close to all plants to prevent access via surrounding vegetation. Ants were excluded on 2 July, 12 July, and 29 June in 1998, 1999, and 2001, respectively. Different plants were used each year.

After establishing the treatments we surveyed the plants weekly. We counted the number of ants, membracid nymphs, and membracid adults. Once nymphs began approaching final instar we used a painter's Speedball opaque paint marker (Speedball Art Products, Statesville, North Carolina, USA) to place a dot on the pronotum of membracid adults; this allowed us to determine the number of newly emerged adults each week.

Spatial variation experiment

In the summer of 2001, we established five separate field sites 25×10 m in size. Each of these five sites was located along a 5 km transect, with adjacent sites between 0.5 km and 1.5 km apart. One of these sites, Site E, was used in the temporal variation experiment. The experiment was set up in late June just as nymphs were emerging from eggs. At each of these sites we tagged between 20 and 40 *C. viscidiflorus* plants that had evidence of membracids (i.e., either nymphs or oviposition scars were present). On 29 June ants were excluded from half of the plants.

Beginning 3 July and ending the week of 2 September, we surveyed the plants weekly. At each survey we counted the number of ants, membracid nymphs, membracid adults, and noted the presence/absence of spiders in weeks 2 through 8. We also assessed the phenology of the plants; categorizing plants as without reproductive parts, with buds, with flowers, or with mature seeds. Beginning with week 3 of surveying, we marked adult membracids.

To determine if the number of ants present at each site had an effect on membracid survivorship, ant density was assessed at each site by baiting the ants with canned tuna fish. On 23 July, at each of the five 25×10 m field sites, we placed 16 bait stations spread out in a grid pattern; each consisted of a tablespoon of tuna on an index card. Each bait station was surveyed after two hours.

Analysis

We analyzed temporal variation with a two-way ANOVA, with year and treatment as single factors. New adult production was the response variable. We added 1 and log-transformed this number because adult production was roughly a lognormal distribution.

We used repeated-measures ANOVA to determine whether the effect of ants on nymph numbers varied among sites with time in 2001. Specifically, nymph number on each of the plants was the repeated measure. Because nymph number was an approximately lognormal distribution, we log-transformed nymph number after adding 1. We included site and treatment as fixed, independent effects. The analysis was performed on nymph number through the first eight surveys because nymph number was not counted in week 9 and there were some missing plants in week 10.

Additionally, we used two-way ANOVA to determine whether the effect of the ants on the membracids, as measured by the number of new adults emerging on each plant, varied among sites. We analyzed the log-transformed data of total new adult production after adding 1, with ant treatment and site as fixed effects.

We tested for the presence of density dependence between nymph number and new adult production by regressing the number of new adults on the maximum number of nymphs found on plants across the surveys (log-log transform). If density dependence is present and the y-intercept is zero, the regression coefficient from a linear regression of the log-transformed data of the two variables will be significantly different from 1 (Billick 2001).

To estimate average phenology for each site, we assigned a numerical value to each of the phenological categories (1 = budding, 2 = flowering, etc.) in week 6 (chosen because plants displayed considerable variability in phenology at this time) and calculated the average value of the plants for each site. We used contingency analysis to determine whether phenological stage varied among sites. We estimated spider density

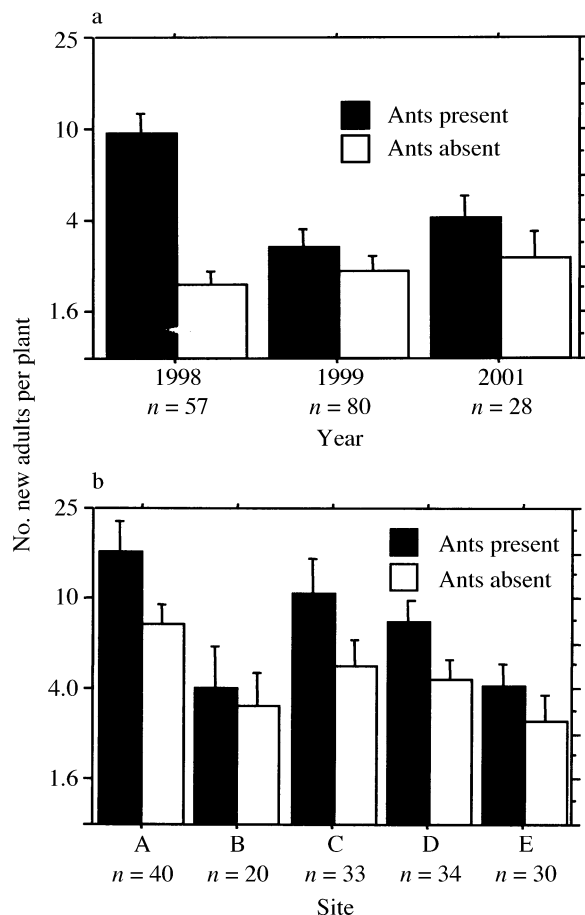


FIG. 1. (a) The mean number of new adults produced on plants at a single site in three different years. Both year and the presence of ants affected new adult production ($F_{2,159} = 4.3$, $P = 0.01$, and $F_{1,159} = 18$, $P < 0.0001$, respectively). There was also a strong year \times ant interaction ($F_{2,159} = 7.4$, $P < 0.001$). (b) The mean number of new adults that emerged per plant at the five different sites. The site affected new adult production ($F_{4,147} = 6.5$, $P < 0.0001$). Ant tending increased new adult production ($F_{1,147} = 8.7$, $P = 0.004$), but the effect of the ants did not vary by site ($F_{4,147} = 0.36$, $P = 0.84$). The number of new adults per plant was transformed by adding 1 and taking the logarithm for purposes of statistical analysis. To be consistent, the figure is shown with the y-axis on a log scale, and 1 has been added to the pre-transformed values. Because the range of the means is less than one order of magnitude, increments between tick marks represent 0.4 orders of magnitude rather than one order of magnitude. Sample size is represented by n . Means are shown ± 1 SE.

by calculating the percentage of plants with spiders from the seven spider surveys and rank ordered the sites. We then calculated the average rank of the six surveys for each site. To determine whether sites consistently varied in the spider ranking, we used a Kruskal-Wallis test, with site as the independent variable. We estimated ant density by simply summing the number of ants on the bait stations from the survey at each site and used one-way ANOVA to determine if sites varied in ant densities. Finally, we calculated the av-

erage per capita tending rate by taking the average per capita tending rate (number of ants divided by the number of nymphs) for each plant for the first six weekly surveys. We then averaged across plants within each site to generate a single estimate for each site.

To determine whether phenology, spider density, ant density, or per capita ant tending explained variation in the effect of the ants on the membracids, we performed a nonparametric Kendall's coefficient of rank correlation analysis. We estimated the effect of the ants on the membracids by using nymph numbers in week 3, the last survey before nymphs began emerging into adults. We divided the mean number of nymphs on plants with ants by the mean number of nymphs on plants without ants within each site. We also estimated the effect of the ants on the membracids in similar fashion by using total adult production instead of the number of nymphs present in week 3. We then correlated both response variables, total adult production and nymph numbers in week 3, with the phenology, spider density, ant number at baits, and per capita tending estimates of each site.

RESULTS

Temporal variation

New adult production varied significantly among years (Fig. 1a: 1998, $x = 7.8$, $SE = 1.5$; 1999, $x = 4.0$, $SE = 0.73$; 2001, $x = 4.1$, $SE = 0.84$). Ants increased new adult production over 300% when averaged across all years, though there was also a significant year \times treatment interaction. The ant effect was strongest in 1998, increasing new adult production over 800%, compared to a 200% increase in 1999 and a 33% increase in 2001.

Spatial variation

The mean number of nymphs per plant was highest, 35.6 nymphs per plant ($SE = 4.3$), on the first weekly survey and declined to a low of 4.8 nymphs per plant ($SE = 0.97$) on the last survey. Because the number of nymphs remaining was so low on the final census, further surveys would not have changed the following results. There was no difference in nymph numbers between ant and no-ant treatments on the first survey ($F_{1,147} = 0.60$, $P = 0.44$). Through time, nymph number varied both among sites and between ant treatments (see Table 1 for a summary of the analysis). There was a marginally significant site \times treatment interaction, suggesting the effect of the ants varied by sites. Finally, all of the effects, including the interaction between site and treatment, varied with time. New adult production per plant ranged from zero to 96 new adults ($SE = 1.3$), with a median of 6 adults. Both ant tending and the site had strong effects on new adult production, but unlike nymph number, there was no evidence that the effect of the ants varied by site (Fig. 1b). There was strong negative density dependence in new adult pro-

TABLE 1. Repeated-measures ANOVA: the effect of site and *Formica obscuripes* ants on *Publilia modesta* nymph number.

| Source of variation | df | MS | F | P |
|---------------------------------------|------|-------|------|---------|
| Site | 4 | 26.0 | 20.0 | <0.0001 |
| Ant treatment | 1 | 18.0 | 14.0 | 0.0002 |
| Site \times Ant treatment | 4 | 2.9 | 2.3 | 0.06 |
| Plant | 147 | 1.3 | | |
| Week | 7 | 4.7 | 51.0 | <0.0001 |
| Week \times Site | 28 | 0.27 | 2.9 | <0.0001 |
| Week \times Treatment | 7 | 0.38 | 4.1 | 0.0002 |
| Week \times Site \times Treatment | 28 | 0.20 | 2.2 | 0.0002 |
| Week \times Plant | 1029 | 0.093 | | |

duction. The regression coefficient of the log of new adult production on the log of maximum nymph number was significantly less than 1 (Fig. 2). The sites differed in how quickly plants reached the flowering stage ($\chi^2 = 22$, $df = 4$, $P = 0.0002$); the sites ranged from 42% of plants flowering at Site A to 87% of plants flowering at Site B during the survey in week 6. Sites also consistently varied in the percentage of plants that had spiders (Kruskal-Wallis: $H = 15$, $df = 4$, $P = 0.004$). Sites varied considerably in the number of ants that visited baits ($F_{4,75} = 10.7$, $P < 0.0001$; Site A: $x = 16.9$, $SE = 2.0$, $n = 16$; Site B: $x = 18.3$, $SE = 4.0$, $n = 16$; Site C: $x = 42.1$, $SE = 4.6$, $n = 16$; Site D: $x = 39.3$, $SE = 4.2$, $n = 16$; Site E: $x = 30$, $SE = 2.0$, $n = 16$). This variation in ants at baits was reflected in differences in per capita tending rates; the number of ants per nymph varied significantly among sites (Kruskal-Wallis: $H = 23.7$, $P < 0.0001$, $df = 4$; Site A: $x = 0.46$, $SE = 0.09$, $n = 20$; Site B: $x = 0.57$, $SE = 0.79$, $n = 6$; Site C: $x = 1.4$, $SE = 0.6$, $n = 14$; Site D: $x = 0.37$, $SE = 0.58$, $n = 15$; Site E: $x = 1.0$, $SE = 0.1$, $n = 14$).

The effect of the ants on the membracids was not significantly correlated with the number of spiders

(Kendall's coefficient of rank correlation: nymphs, $\tau = -0.2$, $P = 0.62$; adults, $\tau = -0.6$, $P = 0.14$), the number of ants at baits (nymphs, $\tau = 0.2$, $P = 0.62$; adults, $\tau = 0.6$, $P = 0.14$), per capita tending (nymphs, $\tau = 0.4$, $P = 0.33$; adults, $\tau = 0.0$, $P = 0.99$), or plant phenology (nymphs, $\tau = 0.4$, $P = 0.33$; adults, $\tau = 0.4$, $P = 0.33$). When per capita tending levels were examined on a plant level instead of a site level, mean per capita tending rates did not affect the number of new adults produced ($\tau = -0.085$, $P = 0.3$, $n = 69$).

DISCUSSION

This study provides further evidence that the strength of the positive effect of *Formica obscuripes* on *Publilia modesta* varies temporally. The mechanism underlying the variation is not clear. Salticid spiders have been identified as an important predator of membracids (Cushman and Whitham 1989, Del-Claro and Oliveira 2000) and there is evidence that one of the main benefits of ant tending at this site is protection from spiders (J. Reithel, *unpublished data*). Indeed, Cushman and Whitham (1989) suggest that temporal variation in salticid density generated the conditionality observed in their study. Other factors, however, such as yearly variation in ant foraging patterns could be just as important.

It is highly unlikely that our results are an artifact of differences in sampling among years. As in other similar studies (Cushman and Whitham 1989, Del-Claro and Oliveira 2000) we used standardized techniques in all three years. Additionally, we set up the experiments at approximately the same time relative to the phenology of the membracids in each year. The date the experiment was set up in 1998, the year that was most different from the other two years, was bracketed by the set-up dates of the other two years. Thus the date of set up did not influence our estimates of the effect of the ants on the membracids in any obvious way.

Whether or not the mutualism varied spatially depended upon the measure of fitness used in the analysis. The effect of ants on nymph number varied at the different sites. When we extended our analysis to a more complete measure of fitness, new adult production, we failed to detect spatial variation in the effect of ants.

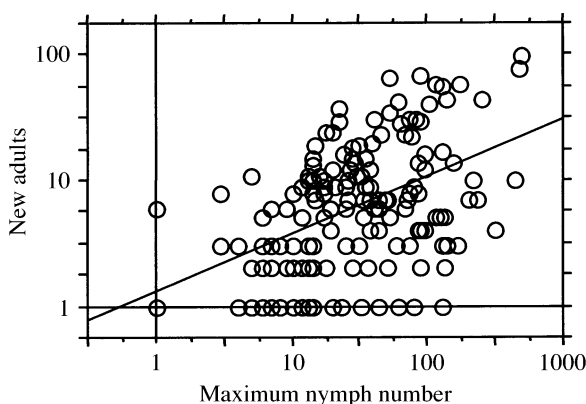


FIG. 2. The relationship between the maximum number of nymphs and new adult production, plotted on a logarithmic scale. There was strong negative density dependence, with larger nymph aggregations producing proportionately smaller numbers of new adults. The slope of the regression was significantly different from 1 ($P < 0.0001$, $n = 157$). Regression coefficient = 0.46 ± 14 (95% confidence limits).

The apparently paradoxical result can be explained by the negative correlation between aggregation size and adult production. While ant-tended aggregations had higher nymph survivorship leading to larger aggregations, larger aggregations produced proportionately fewer new adults (Fig. 2). Thus, negative density dependence washed out spatial variation in the effect of ants on total fitness of membracids. Spatial variation in the magnitude of the benefit of ants on nymph numbers did not translate into variation in the magnitude of the benefit on adult production. Negative density dependence is common in homopteran aggregations (Addicott 1979, Breton and Addicott 1992, Morales 2000a). Consequently, the results of this study are an important extension of previous work (Cushman and Whitham 1989, Del-Claro and Oliveira 2000) that relied upon measurements of nymph numbers and not adult numbers to detect temporal conditionality in ant-membracid mutualisms.

Additionally, our estimate of total adult production allowed us to test directly the hypothesis of a year \times treatment interaction. Because previous studies (Cushman and Whitham 1989, Del-Claro and Oliveira 2000) relied upon repeated measures of nymph numbers, those studies were only able to test for a treatment effect in each of the years separately. Finding a treatment effect in some years but not others, however, is not strong evidence of a year \times treatment interaction (Sokal and Rohlf 1981). For example, if we analyze the effect of ants at the different sites separately, we find ants significantly affected new adult production in two of the five sites. In contrast, directly testing for differences among sites found no site \times ant effect interaction (Fig. 1b). The experimental design of this study allowed us to demonstrate, however, that the general finding of temporal variation in effect of ants is robust to a more rigorous statistical analysis.

The inability to detect a site \times treatment interaction in new adult production was undoubtedly affected by the scale of the spatial study. Sites at far distances are more likely to have greater differences in the phenology of the species involved as well as tending patterns in ants and the species and density of predators. *Publilia modesta* is distributed broadly throughout much of the Midwest and the West within the United States (Kopp and Yonke 1973) and it would be extremely surprising if variation in the nature of the mutualism could not be detected on that scale.

While the scale of this study is extremely small relative to the scale of the treehopper's range, the lack of variation in the effect of the ants on the membracids over several kilometers is interesting from an evolutionary perspective. Little is known about effective dispersal rates in treehoppers in general, though the propensity of both adults and nymphs of *P. modesta* to stay on a single plant suggests movement rates of *P. modesta* are low. *Publilia modesta* is extremely patchy in suitable habitat throughout the Gunnison Basin; al-

most identical locations, often in close proximity, will vary considerably in *P. modesta* density. In many cases, what appears to be ideal habitat completely lacks *P. modesta*. Additionally, nymphs and adults cluster around ant colonies because of the importance of ants to survivorship (McEvoy 1979, Morales 2001), making effective dispersal over large distances less likely. Thus there is reason to believe that populations several kilometers apart are isolated. Consequently, spatial variation in the effect of the ants on the membracids on the scale of several kilometers, were it to exist, would be evolutionarily meaningful.

The lack of spatial variation in the ant effect of new adult production was not for a lack of differences among sites. The sites differed in all four of the characteristics we measured (i.e., the number of ants foraging at the site, the per capita number of ants tending treehoppers, the number of spiders found on host plants, and the phenology of host plants). While there were differences among sites in the effect of ants on nymph numbers in week 3, the differences in the effect of the ants on nymph numbers were not related to the differences in site characteristics that we measured. With only five sites, there was limited statistical power to detect a correlation between site characteristics and the effect of ants on membracids; a nonparametric correlation would have to be 0.80 in order to be significant. While a sample size of five reduced our statistical power, we gained statistical power by replicating measurements within sites and reducing our sampling error in estimates of site characteristics. Given our robust estimates of site characteristics, if variation in the effect of the ants on the membracids could be explained in a simple way by a single factor, we should have detected such a relationship. Thus despite detectable differences among sites, differences in site characteristics did not translate into spatial variability in the effect of ants on membracids. Temporal variation was the primary factor generating conditionality in the mutualism between *P. modesta* and *F. obscuripes*.

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