

Abiotic and Multitrophic Determinants of Geographic Distribution in an Herbivorous Insect

Joseph S. Phillips

Mentor: Kailen Mooney

Abstract

Characterizing the factors that determine the geographic range limits of species is a major goal of ecology. Historically, abiotic factors (e.g. light environment) have been the focus of research of species geographical distributions. While recent work has shown that pairwise species interactions (e.g. predation) are also important for determining these distributions, the combined action of interactions spanning multiple trophic levels and the environmental mediation of such interactions are poorly understood. In this study, we explored the mechanisms by which light environments influence aphid population growth, focusing on (1) direct or plant mediated effects of light, (2) variation in predation pressure across a light gradient, in the absence of ants, and (3) variation in ant tending across a light gradient. Our results show that aphid population perform better in high light environments because of increased tending of ants, which reduces predation pressure. This work demonstrates that understanding the consequences of abiotic factors on population performance (and, hence, species range limits) requires considering how they mediates ecological interactions in a community context.

Introduction

Characterizing the factors that determine the geographic range limits of species is a major goal of ecology (MacArthur 1984; Gaston 2009; Scheiner & Willig 2011). Furthermore, an understanding of these factors and how they might interact with changing environments is central for managing ecosystems and conserving biodiversity (Van der Putten et al. 2010). A wide range of ecological processes is likely to be important in influencing range limits. Consequently, numerous studies have explored how a variety factors (genetics, physiology, behavior, interspecific interactions, climate, etc.) operating at multiple scales of biological organization may be important for determining range limits (Gaston 2003).

Abiotic factors (such as climate) have a strong influence on organismal reproduction and survival and have been a major focus of attempts to model species' geographic ranges (Guisan & Zimmerman 2000; Pearson & Dawson 2003; Guisan & Thuiller 2005). However, there is growing recognition that trophic interactions should be incorporated into these models (Gaston 2009; Van der Putten et al. 2010; Holt & Barfield 2011). Predation and herbivory are known to exert strong top-down control on a wide range of terrestrial and aquatic communities (Werner 1983; Sih et al. 1985; Carpenter et al. 1985; Sih et al. 1998; Pace et al. 1999). Nonetheless, top-down effects have typically been assumed to play a relatively limited role in determining species range limits. This is based primarily on the belief that specialist enemies would go locally extinct after

eliminating their prey, thus preventing them from exhibiting consistent exclusion of the prey population (Gaston 2009).

However, recent theory suggests that both specialist and generalist enemies can have a wide range of positive and negative effects on species distributions, depending on the community context and the extent of predator and prey dispersal (Holt & Barfield 2011). Field experiments suggest that predation can play an important role altering prey habitat choice (Werner et al. 1983; Louda & Rodman 1996). Louda & Rodman (1996) demonstrated that intense insect herbivory in sunny habitats restricts bittercress (*Cardamine cordifolia*) to shady habitats. When habitat use varies across a spatially heterogeneous landscape due to predation, it can strongly influence a species' range limits (Pienkowski 1984; Bruelheide & Scheidel 1999; deRivera, et al. 2005).

While these studies provide important evidence for the role that trophic interactions can play in determining species distributions, they are limited by their consideration of isolated pair-wise interactions. Ecological systems are characterized by the action of multiple processes that may interact with each other (Polis & Strong 1996; Van der Putten et al. 2010). For example, multiple predators can have non-additive effects on prey, either by lowering prey risk through predator-predator interactions (i.e. interference or intraguild predation) or raising prey risk by inducing conflicting prey defenses (Sih et al. 1998). Bittercress (*Cardamine cordifolia*) restriction to shady environments due to altered action of herbivores in the shade versus the sun is an example of how biotic and abiotic factors can interact to alter prey habitat selection (Louda & Rodman 1996). Given the non-additivity of ecological processes, a major challenge in understanding species range limits is characterizing the simultaneous action and potential interactions between these diverse processes (Gaston 2009).

Protection mutualisms are situations where one organism protects another organism from consumers in exchange for resources (e.g. ant protection of hemipterans from predators in exchange for honeydew). By their nature, these interactions entail the relationship between multiple ecological factors spanning different trophic levels (reviewed in Stadler & Nixon 2005; Ness et al. 2009). Consequently, the nature of these mutualisms is known to be highly dependent on the context in which they occur. For example, Petry et al. (2012) demonstrated that ants fed an excess of carbohydrates ceased tending aphids (defending aphids from predators in exchange for food), showing how factors such as diet can mediate mutualistic interactions. Another study demonstrated that the antagonistic and mutualistic effects of ants combined with host plant genetics influence the competitive interactions between three aphid species (Smith et al. 2008). Since the outcome of these interactions can have important effects on the fitness of protected mutualists (Kaplan & Eubanks 2005), they may be important for determining species persistence in different habitats. Therefore, protection mutualisms provide a valuable context for exploring how the interaction between multiple processes influence species range limits.

In this study, we explored how the abiotic environment mediated multitrophic interactions of the aphid *Aphis helianthi* (Hemiptera: Aphididae), and whether this in turn influenced this herbivore's range limits. This insect is found throughout the Rocky Mountains region, primarily on the host plant *Ligusticum porteri* and other members of Apiaceae (Palmer 1952). This aphid has a number of arthropod predators, including lady beetles (Coccinellidae) and mites (Acari), and is tended by ants in the genus *Formica*

(Hymenoptera: Formicidae). *Aphis helianthi* is only commonly found in alpine meadows, despite the fact that *L. porteri* and *Formica* ants are found in both meadows and Aspen understory. Interestingly, when *A. helianthi* is found in the aspen understory, the ants appear to tend them less often (Unpublished data). We hypothesized that in the absence of the anti-predator defense that ant tending provides, *A. helianthi* is unable to persist in the aspen understory. While many factors differ between aspen groves and alpine meadows, light availability (and associated factors, such as temperature) seems most likely to mediate ant-aphid interactions.

We explored how light mediates aphid interactions with ants and predatory arthropods by artificially excluding different sets of arthropods across a natural light gradient. Specifically, we assessed the effects of the following factors on aphid population growth: (1) abiotic factors associated with light variation (e.g. temperature) in the absence of other arthropods, (2) predators across a light gradient in the absence of ants, and (3) ants across a light gradient. Our results shed light on how the combined action of abiotic factors and species interaction across multiple trophic levels affect population aphid growth, with implication for the determinants of aphid geographic range limits.

Experimental Methods

This study was conducted in alpine meadows and aspen groves near the Rocky Mountain Biological Laboratory in Gunnison County, Colorado. We selected 15-16 naturally occurring *L. porteri* from six different sites, with varying light levels, for a total of 94 plants. On July 1st 2013, colonies of 10 aphids each were established on the terminal umbel of each plant and allowed to establish and reproduce for one week before the application of the experimental treatments. During this initial period, all predators and mutualists were excluded by enclosing each aphid colony in a mesh bag, and by wrapping each plant stem in masking tape coated with Tanglefoot (Contech Inc.) At the end of this period, some of the aphid populations declined in size, with some instances of extinction. Populations with fewer than 10 individuals were again inoculated with aphids to establish population sizes of 10. This resulted in initial populations ranging from 10-123 aphids (mean= 31.489; standard error=2.267). These population sizes were used as the initial abundances for all subsequent analysis.

On July 8th, each colony was randomly assigned to one the following treatments, such that each site had approximately equal representation of each treatment: control (“no exclusion”; open to ants and predators), exclusion of all arthropods (“total exclusion”), and ant exclusion only (“ant exclusion”; open to predators). The no exclusion colonies were enclosed in mesh bags with slits to control for the effect of bags on the umbel. For total exclusion, each colony was enclosed in a fine mesh bag and each plant stem was wrapped with masking tape coated with Tanglefoot. The ant exclusion was similar, but for two modifications: slits were cut in each bag to allow access by aerial predators and small segments of flat toothpicks were placed underneath the tape to allow small predatory arthropods (i.e. mites) to pass through, while preventing access to ants. Aphid population size, ant abundance, and predator abundance were assessed on July 11th, July

14th, and July 18th. Predators included various hemipterans known to feed on aphids, parasitoid wasps, spiders, and mites.

Between 10AM and 12PM on a cloudless day (July 31st 2013), photosynthetically active radiation (PAR) was recorded for each plant at the height of the focal umbel. Light levels were measured using a LightScout Light Sensor Reader with Quantum Light Sensor (Spectrum Technologies). Due to the large variation in light levels within each site, the average light level for each site was used for all analyses. Light levels ranged between 224.81 $\mu\text{E}/\text{m}^2/\text{sec}$ and 1303.2 $\mu\text{E}/\text{m}^2/\text{sec}$ (mean= 743.12 $\mu\text{E}/\text{m}^2/\text{sec}$).

To assess the differences in ant communities between sites, we collected samples using pitfall traps at each site. Pitfall traps were constructed from 50mL plastic centrifuge tubes filled with a mixture of water and dish soap. Each trap was placed into the substrate so that the lip of the trap was flush with the soil surface. Traps were set on July 6th and left in place for 48 hours before collected. Ants were sorted into one of the following taxonomic groupings and counted: *Formica fusca* group (Formicinae), *Formica rufa* group (Formicinae), *Lasius spp.* (Formicinae), *Tapinoma sessile* (Dolichoderinae), *Myrmica spp.* (Myrmicinae) and other. We also recorded the total number of predatory mites collected in each trap.

Statistical Methods

Arthropod abundance

The effects of light levels and exclusion treatments on arthropod abundance were assessed using a series of generalized linear models (GLMs). Analysis of count data is typically done using Poisson or negative binomially distributed errors (Zeileis et al. 2008). However, since our data contained a substantial number of 0 values, we compared the results from these classic models to two modified models: hurdle models and zero inflation models, each performed with Poisson and negative binomial distributions (Zeileis et al. 2008). The models with the lowest AICs (Akaike information criterion) were selected as the optimal models and used for subsequent analysis. Ant and predator abundances we calculated as the cumulative number of individuals counted on each plant from July 11th to July 18th, except where otherwise noted. Light was treated as a continuous variable, with the average value for a particular site used for all plants at that site (see Experimental Methods).

(a) Effects of exclusion on ant tending and predator abundance

We assessed the effect of ant exclusion and total exclusion on ant tending of aphids by fitting GLMs using ant abundance on each plant as the response variable and exclusion treatment as the explanatory variable. A similar procedure was used to assess the effect of exclusion on predator abundance on each plant. We noted a substantial increase in the number of predators on each plant over the last sampling period; therefore, we performed the analysis again using predator abundance from July 11th to July 14th.

(b) Effect of light levels on ant abundance (Pitfall traps)

To determine how the natural abundance of ants varies with light levels, we fit GLMs using ant abundance in pitfall traps as the response variable and light level as the explanatory variable.

(c) Effect of light levels on ant tending

To determine how ant tending of aphids varies with light levels, we fit GLMs using ant abundance on each plant as the response variable and light level as the explanatory variable.

(d) Effects of light levels on predator abundance

To determine how overall predator pressure varies with light levels in the absence of ants, we fit GLMs using predator abundance on each plant from the ant exclusion treatment as the response variable and light level as the explanatory variable. A similar procedure was used to assess the effect of light level on mite abundance in pitfall traps.

(e) Effects of ant tending on predator abundance

The effect of ant tending on predator pressure was assessed by fitting GLMs using predator abundance on each plant as the response variable and ant abundance on each plant as the explanatory variable.

Aphid population growth rate

The effects of light and arthropod exclusion on aphid population growth were assessed using GLMs, with aphid per capita population growth rate (r) as the response variable. Per capita growth rates were calculated as $r = \ln(N_0/N_t)/t$, where N_0 is the initial population size, and N_t is the population size at time t . For the following analyses, r was calculated from July 8th to July 18th. In our analysis, we assumed normal distributions, which are consistent with visual inspection of our data. Light was treated as a continuous variable, with the average value for a particular site used for all plants at that site (see Experimental Methods).

(a) Effects of light level on per capita growth rate

To determine whether light (and correlated abiotic factors) has a direct effect on aphid population growth, we analyzed data from the total exclusion treatment, using light level as the explanatory variable.

(b) Effects of predators on per capita growth rate

To determine whether the effect of predators varies with light level in the absence of ants, we analyzed data from total exclusion and ant exclusion, using light level, exclusion treatment, and their interaction as explanatory variables.

(c) Effects of ants on per capita growth rate

To determine whether the effect of ants varies with light level in the presence of predators, we analyzed data from no exclusion and ant exclusion, using light level, exclusion treatment, and their interaction as explanatory variables. Since some ants were present in the ant exclusion treatments (see Results), we also performed this analysis using ant presence in place of exclusion treatment.

Results

Arthropod abundance

For every set of analyses of arthropod abundance, the classic GLM, hurdle model, and zero-inflation model with negative binomially distributed errors had nearly identical AICs, which were substantially lower than those for the models with Poisson distributed errors (Appendix I). In general (with exceptions noted below), the optimal models gave similar results; therefore, we only report the results of the classic GLM.

(a) Effects of exclusion on ant tending and predator abundance

For the classic GLM, there was a significant effect of total exclusion on ant tending, but not of ant exclusion ($p=0.0141$ and $p=0.607$, respectively; $df=89$; $\text{mean}_{\text{no exclusion}}=2.516$, $\text{mean}_{\text{total exclusion}}=0.387$, and $\text{mean}_{\text{ant exclusion}}=1.733$; Fig 1). (For the hurdle and zero-inflation models, there was not a significant effect of either total exclusion or ant exclusion.) However, the mean number of ants for the no exclusion treatment was 45% higher than that for the ant exclusion treatment, suggesting a lack of sufficient sample size to detect a significant effect. Furthermore, the majority of ants seen in the total and ant exclusion treatments were *Tapinoma sessile*, while other ant taxa were seen almost exclusively on plants with no exclusion (Fig. 2).

There was no significant effect of either total or ant exclusion on predator abundance from July 8th to July 18th ($p=0.483$ and $p=0.152$, respectively; $df=91$; $\text{mean}_{\text{no exclusion}}=5.677$, $\text{mean}_{\text{total exclusion}}=4.710$, and $\text{mean}_{\text{ant exclusion}}=3.875$). However, for predator abundance from July 8th to July 14th, there was a significant effect of total exclusion, but not ant exclusion ($p=0.00522$ and 0.09341 , respectively; $df=91$; $\text{mean}_{\text{no exclusion}}=2.387$, $\text{mean}_{\text{total exclusion}}=1.161$, and $\text{mean}_{\text{ant exclusion}}=1.594$; Fig 1.).

(b) Effect of light levels on ant abundance (Pitfall traps)

For the classic GLM (and hurdle model), there was a marginally non-significant positive effect of light level on ant abundance in pitfall traps, while in the zero-inflation model the effect was significant (slope=0.00116 and 0.000962; $p=0.068$ and 0.0476 ; $df=28$ and 25 , respectively; Fig. 3).

(c) Effect of light levels on ant tending

There was a significant positive effect of light level on ant tending of aphids (slope=0.00215; $p=0.0187$; $df=29$; Fig 3).

(d) Effects of light levels on predator abundance

There was no significant effect of light level on overall predator abundance on plants (slope=0.000547; $p=0.189$; $df=30$; Fig 3). However, there was a significant positive effect of light level on mite abundance in pitfall traps (slope=0.00199; $p=0.000191$; Fig 3).

(e) Effects of ant tending on predator abundance

There was a marginally non-significant negative effect of ant tending on predator abundance (slope=-0.0582; $p=0.0511$; $df=90$; Fig 4).

Aphid population growth rate

(a) Effects of light level on per capita growth rate

There was no significant effect of light level on aphid per capita growth rate in the absence of other arthropods (slope= 1.472×10^{-5} ; $p=0.624$; $df=28$; Fig 5).

(b) Effects of predators on per capita growth rate

There was a significant main effect of exclusion treatment on aphid population growth rate, however there was no effect of light or interaction between light and exclusion ($p=0.0325$, 0.653 , and 0.362 , respectively; $df=56$; $\text{mean}_{\text{total exclusion}}=0.0744$ and $\text{mean}_{\text{ant exclusion}}=-0.0407$; Fig 5).

(c) Effects of ants on per capita growth rate

There was no significant main effect of exclusion on aphid population growth rate, however there was a significant main effect of light and an interaction between light and exclusion ($p=0.0738$, 0.0433 , and 0.0431 ,

respectively; $df=48$; $\text{slope}_{\text{light, no exclusion}}=0.0639$ and $\text{slope}_{\text{light, ant exclusion}}=-0.0428$; Fig 5).

Discussion

In this study, we investigated the mechanisms by which light environment affects aphid population growth rates, with implications for aphid geographical distributions. Specifically, we considered three possible mechanisms by which light may affect aphid populations: (1) direct or plant mediated effects of light—i.e. effects in the absence of other arthropods, (2) variation in predation pressure across a light gradient, in the absence of ants, and (3) variation in ant tending across a light gradient. Our results suggest that the former two mechanisms are unlikely to be important for aphid population growth rates. Light environment, in the absence of other arthropods, has no effect on population growth. And while the presence of predators has a substantial effect on aphid populations, there is no variation in abundance or effects of predators across light levels. In contrast, we found a significant positive relationship between ant tending and the benefit of ants with increasing light levels, likely due to a reduction in predation pressure. We also found a positive relationship between light levels and overall ant abundance, which may be responsible for higher tending rates in the sun. Taken together, these results show that ants have an indirect positive effect on aphid populations through predator suppression that is mediated by light environment.

It is surprising that abiotic factors associated with light environment do not have direct consequences on aphid population growth. In particular, light levels are likely correlated with ambient temperature, which is known to have important consequences for ectotherm population growth rates (Deutsch et al. 2008). While adaptation to specific conditions is clearly important, insects tend to have higher performance in warmer environments (Amarasekare & Savage 2012). The absence of a plant-mediated effect of light environment is also surprising. Sunlight is known to have important effects on plant function, which can have consequences for herbivore performance. Given the historical emphasis placed on direct abiotic and host-plant mediated effects on population distribution (Guisan & Zimmerman 2000; Pearson & Dawson 2003; Guisan & Thuiller 2005), the absence of these effects for *A. helianthi* population growth suggests that more attention should be paid to alternative mechanisms.

We also expected to see significant variation in predation pressure with light levels, with possible consequences for aphid population growth. Previous work on the interactions between top-down and bottom-up effects suggests that predation pressure should be positively correlated with primary productivity (Borer et al. 2006). As it is well established that primary productivity is positively related with light availability, we expected predation pressure increase with light levels. However, our results show that predation on *A. helianthi* does not vary with light environment. The mechanisms responsible for this pattern are unclear. It may be that light mediates the abundance or behavior of predatory arthropods in a way counteracts the expected increase due to higher primary productivity. Alternatively, it is possible that the community productivity of our sites does not vary with the light levels explored in this study. Experiments manipulating light levels or other abiotic factors are needed to better characterize the situations when predation pressure should be expected to vary with environmental conditions.

The fact that sunlight alters ant tending of aphids, with consequences for aphid population growth, is consistent with an accumulating body of evidence illustrating the context-dependence of mutualistic interactions (Bronstein 1994; Bronstein et al. 2006; Kier et al. 2010). However, the mechanism through which this effect occurs is unclear. Our data show that ant abundance increases with light levels, suggesting that the variation in ant tending may simply be the consequence of overall variation in ant population density. This pattern of ant abundance is likely mediated by temperature, which is consistent with previous work documenting a reduction in arthropod (including ant) abundance along an elevational gradient due to declining temperatures (Lessard et al. 2011). Consequently, density-mediated variation in ant tending of aphids and other species along environmental gradients may be widespread in nature.

However, it is also possible that light environment has per capita effects on ant behavior. For example, ant nutritional needs may vary across light environments, altering the value of aphid honeydew as a food resource. Such an effect could be the consequence of variation in temperature with light environment, as ants are known to respond to thermal environment in a variety of ways. Alternatively, it is possible that differences in aphid quality (either through direct abiotic or plant-mediated effects) across light levels could alter ant interest in tending. However, our results suggest that these alternatives are unlikely, as differences in aphid quality would likely be translated into differences in population growth, though this may not be the case. While multiple mechanisms may underlie the reduction in ant tending at low light levels, based upon our data the simplest explanation of our findings is that this dynamic is driven by reductions in ant abundance.

Historically, research on species range limits has focused on abiotic factors, biotic habitat features (e.g. vegetation), and a limited set of ecological interactions (e.g. competition). While recent work has demonstrated the importance of trophic interactions for species distributions, the simultaneous action of multiple abiotic and biotic factors across multiple trophic levels is still poorly understood. Our results demonstrate how the interactions between light environment, predation, and mutualism exert a strong influence on aphid population growth rates, with possible implications for their persistence in different habitats. Such consideration of multiple biotic and abiotic factors across trophic levels has critical implications for understanding the processes that define species distributions and how species may respond to global change.

References

- Amarasekare & Savage (2012) A framework for elucidating the temperature dependence of fitness. *Am. Nat.* 179:178-191
- Borer, E. T., B. S. Halpern, and E. W. Seabloom (2006). Asymmetry in community regulation: Effects of predators and productivity. *Ecology* 87:2813-2820.
- Bronstein, J.L., T.E. Huxman, and G. Davidowitz (2006). Plant-mediated effects linking herbivory and pollination. *Ecological Communities: Plant Mediation in Indirect*

Interaction Webs. T. Ohgushi, T.G. Craig, and P.W. Price (editors). Cambridge University Press.

Bronstein, J.L. (1994) Conditional outcomes of mutualistic interactions. *TREE* 9:214-217.

Deutsch, C. J., J. Tewksbury, R. B. Huey, K. Sheldon, C. Ghalambor, D. Haak, and P. R. Martin (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *PNAS* 105:6668–6672.

Gaston, K. J. (2003) *The structure and dynamics of geographic ranges*. Oxford, UK: Oxford University Press.

Gaston, K.J (2009). Geographic Range Limits: achieving synthesis. *Proc. R. Soc. B*. 276:1395-1406.

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8:993-1009.

Guisan, A. and N.E. Zimmerman (2000). Predictive habitat distribution models in ecology. *Ecol. Model.*

Holt, R. and M. Barfield (2011). Trophic interactions and range limits: the diverse roles of predation. *Phil. Trans. R. Soc. B* 365:2025-2034.

Kiers, E.T., T.M. Palmer, A.R. Ives, J.F. Bruno, and J.L. Bronstein (2010). The global breakdown of mutualistic interactions among species. *Ecol. Lett.* 13: 1459-1474.

Kaplan, I. and M. D. Eubanks. (2005). Aphids alter the community-wide impact of fire ants. *Ecology* 86:1640-1649.

Lessard, J.-P., T. E. Sackett, W. N. Reynolds, D. A. Fowler, and N. J. Sanders (2011). Determinants of the detrital arthropod community structure: the effects of temperature and resources along an environmental gradient. *Oikos* 120:333-343

Louda S.M. and J.E. Rodman (1996). Insect herbivory as a major factor in the shade distribution of a native crucifer. *J. Ecol.* 84:229-237.

MacArthur (1984) *Geographical Ecology*. Princeton, NJ: Princeton University Press.

Pace, M.L., J.J. Cole, S.R. Carpenter, and J.F. Kitchell (1999). Trophic cascades revealed in diverse ecosystems. *TREE* 14:483-488.

Palmer, M.A. (1952) *Aphids of the Rocky Mountain Region*. Denver, CO: The A. B. Hirschfeld Press.

- Pearson, R.G. and T.P. Dawson (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob. Ecol. Biogeog.* 12:361-371.
- Petry, W.K., K.I. Perry, and K.A. Mooney (2012). Influence of macronutrient imbalance on native ant foraging and interspecific interactions in the field. *Ecol. Ent.* 37:175-183.
- Polis, G.A. and D.R. Strong (1996). Food web complexity and community dynamics. *Am. Nat.* 147:813-846.
- Scheiner, S.M. and M.R. Willig (2011). *The theory of ecology*. Chicago, IL: University of Chicago Press.
- Sih, A.G., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier (1985). Predation, competition, and prey communities: a review of field experiments. *Annu. Rev. Ecol. Syst.* 16:269-311.
- Sih, A., G. Englund, and D. Wooster (1998). Emergent impacts of multiple predators on prey. *TREE* 13:350-355.
- Stadler, B., and A.F.G. Dixon (2005). Ecology and evolution of aphid-ant interactions. *Annu. Rev. Ecol. Evol. Syst.* 36:345-372.
- Smith, R.A., K.A. Mooney, and A.A. Agrawal. (2008). Coexistence of three specialist aphids on common milkweed, *Asclepias syriaca*. *Ecology* 89:2187-2196.
- Van der Putten, W.H., M. Macel, and M.E. Visser (2010). Predicting species distribution and abundance response to climate change: why it is essential to include biotic interactions across trophic levels. *Phil. Trans. R. Soc. B.* 365:2025-2034.
- Werner, E.E., J.F. Gilliam, D.J. Hall, and G.G. Mittlebach (1983). An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540-1548.
- Zeileis, A., C. Kleiber, S. Jackman (2008) Regression models for count data in R. *J. Stat. Software*.

Appendix I: Comparison of model fits

Comparison of AICs for each series of linear models fit to ant and predator abundance data (see Statistical Methods for details): CNB=classic negative binomial, CP=classic Poisson, HNB=hurdle negative binomial, HP=hurdle Poisson, ZNG=zero-inflation negative binomial, and ZP=zero-inflation Poisson.

(a) Effects of exclusion on ant tending and predator abundance

Ant Abundance

CNB	CP	HNB	HP	ZNG	ZP
233	550	235	324	235	324

Predator Abundance (July 11th to July 18th)

CNB	CP	HNB	HP	ZNG	ZP
505	756	509	707	511	339

Predator Abundance (July 11th to July 14th)

CNB	CP	HNB	HP	ZNG	ZP
331	342	336	339	336	339

(b) Effect of light levels on ant abundance (Pitfall traps)

CNB	CP	HNB	HP	ZNG	ZP
222	836	224	722	225	339

(c) Effect of light levels on ant tending

CNB	CP	HNB	HP	ZNG	ZP
111	204	114	151	114	722

(d) Effects of light levels on predator abundance

CNB	CP	HNB	HP	ZNG	ZP
162	211	166	200	166	200

(e) Effects of ant tending on predator abundance

CNB	CP	HNB	HP	ZNG	ZP
493	746	489	690	489	690

Figures

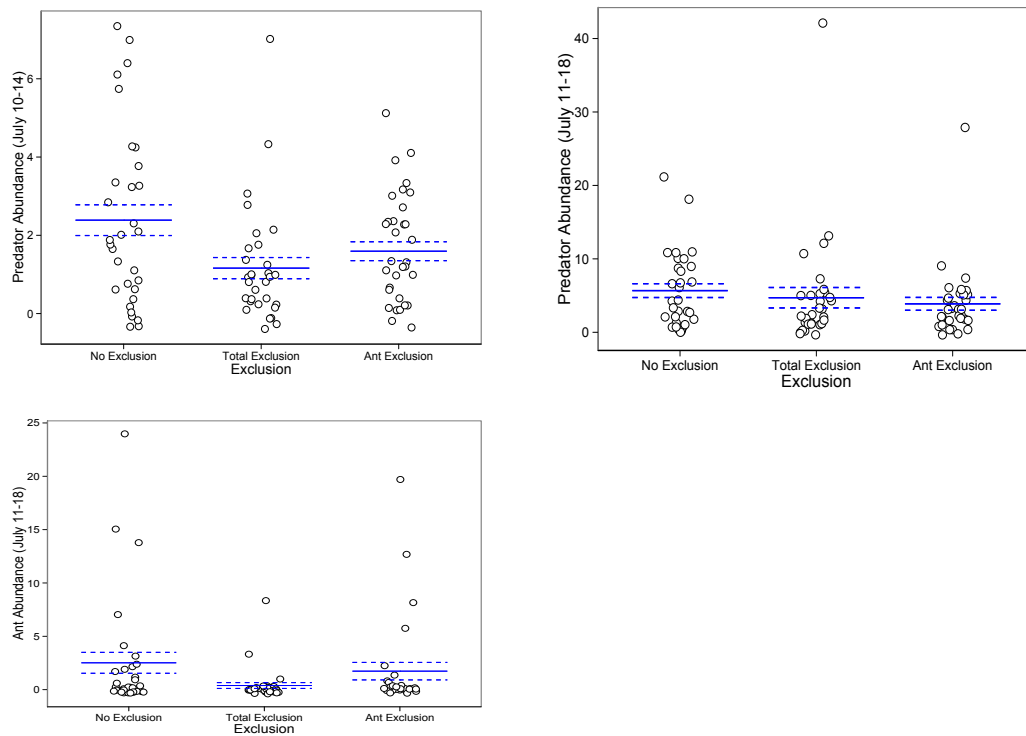


Fig. 1 Effect of exclusion treatments on cumulative ant and predator abundances on plants. Solid and dashed blue lines show means with standard errors.

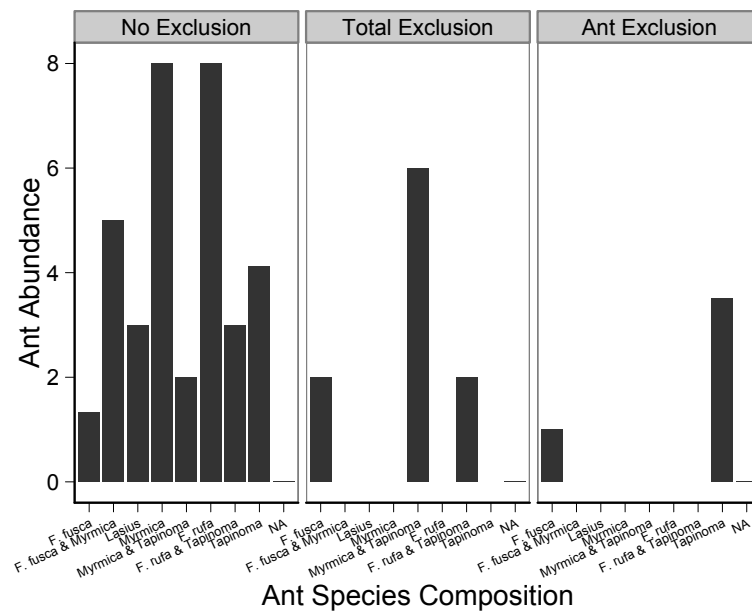


Fig 2. Mean cumulative ant abundance from July 11th to Jul 18th by taxonomic group and exclusion treatment. Bars corresponding to multiple ant taxa reflect instances when multiple taxa were present on a single plant.

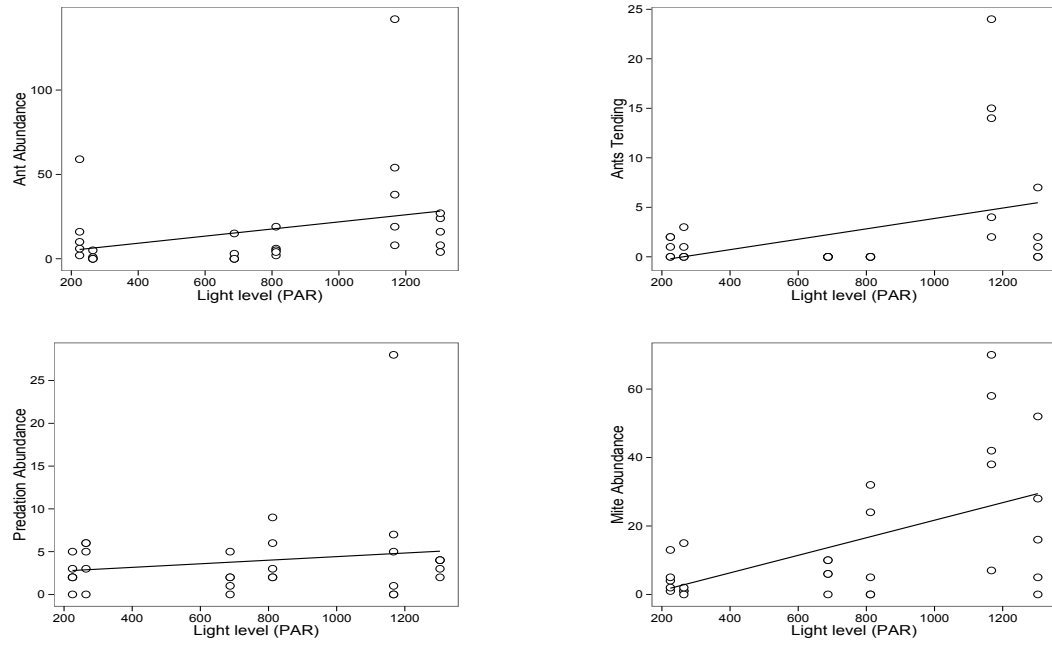
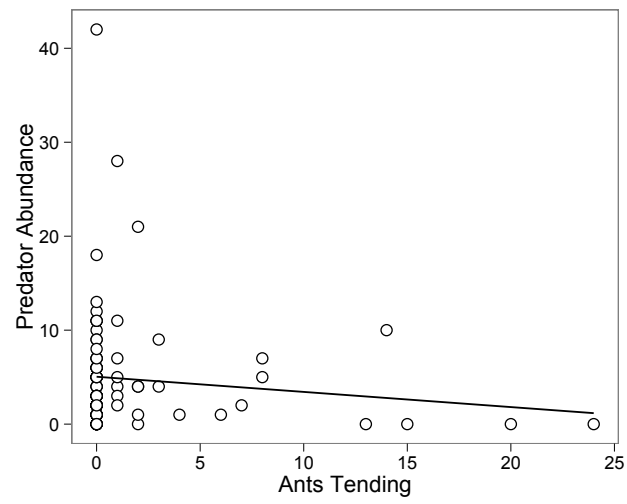


Fig. 3. Effect of light level on cumulative arthropod abundance from July 11th to July 18th. Lines are the best fit lines using QR decomposition.



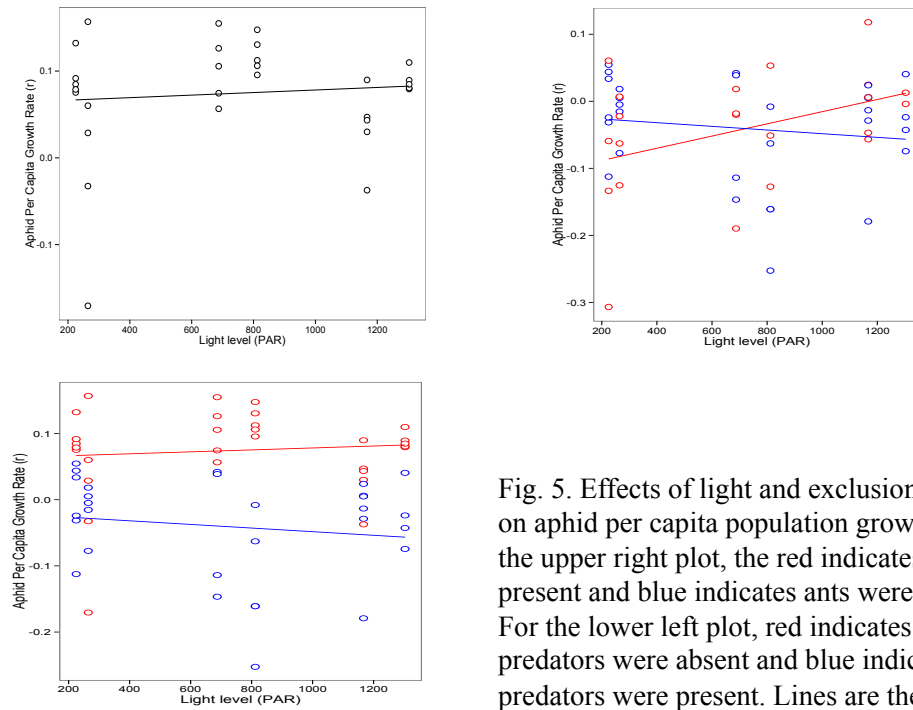
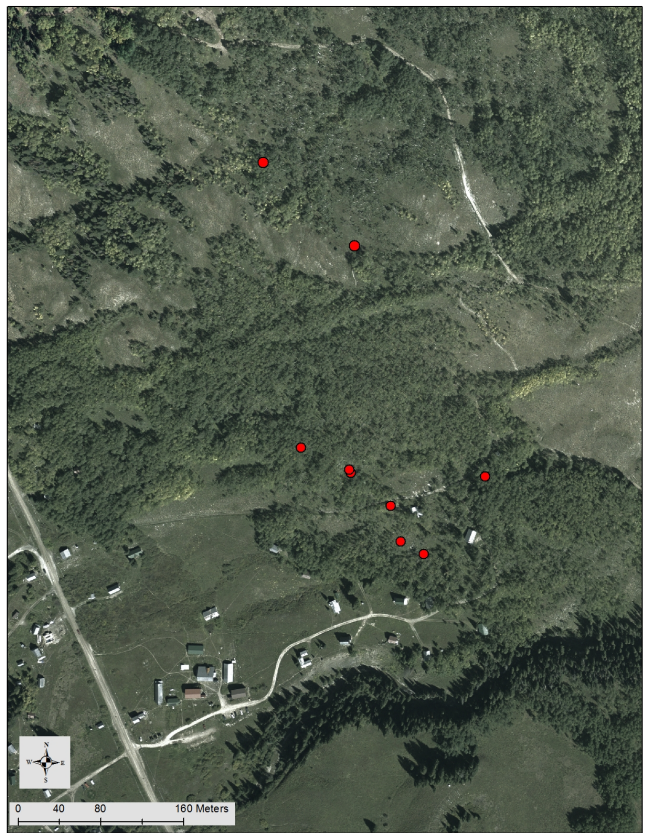


Fig. 5. Effects of light and exclusion treatment on aphid per capita population growth rate. For the upper right plot, the red indicates ants were present and blue indicates ants were absent. For the lower left plot, red indicates that predators were absent and blue indicates that predators were present. Lines are the best fit lines using QR decomposition.



Appendix II. Map of research sites. Site are encompassed within the red circles