Direct and indirect effects of warming on aphids, their predators, and ant mutualists

Brandon T. Barton[1] and Anthony R. Ives

Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706 USA

Abstract. Species exist within communities of other interacting species, so an exogenous force that directly affects one species can indirectly affect all other members of the community. In the case of climate change, many species may be affected directly and subsequently initiate numerous indirect effects that propagate throughout the community. Therefore, the net effect of climate change on any one species is a function of the direct and indirect effects. We investigated the direct and indirect effects of climate warming on corn leaf aphids, a pest of corn and other grasses, by performing an experimental manipulation of temperature, predators, and two common aphid-tending ants. Although warming had a positive direct effect on aphid population growth rate, warming reduced aphid abundance when ants and predators were present. This occurred because winter ants, which aggressively defend aphids from predators under control temperatures, were less aggressive toward predators and less abundant when temperatures were increased. In contrast, warming increased the abundance of cornfield ants, but they did not protect aphids from predators with the same vigor as winter ants. Thus, warming broke down the ant–aphid mutualism and counterintuitively reduced the abundance of this agricultural pest.

Key words: Asian ladybeetle Harmonia axyridis; *behavioral observations; biocontrol; climate change; corn leaf aphids* Rhopalosiphum maidis; *cornfield ant* Lasius alienus; *indirect effect; mutualism; predator–prey interactions; species interactions; warming experiment; winter ant* Prenolepis impairis.

Introduction

Anthropogenic climate change has challenged ecologists to predict how the abundance and distribution of organisms will change in the future (Walther et al. 2002, Tylianakis et al. 2008). This task is particularly important for endangered species, species with economic value, and pests (e.g., Bale et al. 2002, Carpenter et al. 2008, Stirling and Derocher 2012, Barton and Ives 2014). Climate change can affect species both directly through physiology and/or behavior, and indirectly by affecting other species with which the focal species interacts. Although research has disproportionately emphasized the direct effects of climate change, the indirect effects of climate change on species are likely to be large (Tylianakis et al. 2008, Gilman et al. 2010, Kiers et al. 2010, Barton and Ives 2014). Therefore, to predict the response of a species to climate change, it is necessary to consider both direct and indirect effects.

Species engaged in mutualistic interactions may be particularly sensitive to climate change because the loss of one species can lead to large costs for its mutualist partner (Bascompte and Stouffer 2009, Kiers et al. 2010, Marquis et al. 2013). This, and the fact that most organisms rely to some degree on

mutualisms (Bronstein et al. 2004), has focused attention on the possible indirect effects of climate change on mutualisms (Stachowicz 2001) and the possibility of mutualism breakdown. The negative impacts of mutualism breakdown, however, may be reduced by functional redundancy (Bronstein et al. 2004, Kiers et al. 2010). Functionally redundant species are those that have the same function within a community; if one species declines in direct response to an environmental change, a functionally similar species can take its place. A concern, however, is that not all species within a guild are perfectly redundant; they may perform the same function but with different vigor. Thus, functional redundancy may in practice be a gradient, with occasional examples of perfect functional redundancy, and the majority of cases only partial (Rosenfeld 2002).

We experimentally investigated the indirect effects of warming on aphids that operate through their mutualistic interactions with two aphid-tending ant species. This allowed us to test whether the two ant species were functionally redundant in terms of their indirect effects on aphids. Corn leaf aphids (*Rhopalosiphum maidis*) are globally distributed agricultural pests that attack maize and other Gramineae species (El-Ibrashy et al. 1972, Foott 1977), and are commonly found in Wisconsin, USA, cornfields. As sap-sucking herbivores, aphids feed exclusively on phloem, which is rich in carbohydrates but poor in

other nutrients like nitrogen (Gray and Fraenkel 1954). Consequently, aphids must ingest and process large amounts of phloem to meet their nutritional requirements, and they expel excess carbohydrates as liquid waste, commonly called "honeydew." Many ant species collect and consume the honeydew (Way 1963). Corn leaf aphids are eaten by a suite of predators, including damsel bugs (*Nabis* sp.), minute pirate bugs (*Orius* spp.), and, most common in our study system, the multicolored Asian ladybeetle (*Harmonia axyridis*). Because these predators reduce aphid abundance, ants often attack predators and defend aphids in what has become a classic example of a resource (honeydew) for service (protection) mutualism.

The effect of ants as mutualists on aphids differs among ant species and environments (Way 1963, Breton and Addicott 1992, Sakata 1995). We have observed two species of aphid-tending ants co-occurring in the cornfields we study. Winter ants (*Prenolepis imparis*) are relatively large, dominant ants that aggressively defend aphids with a potent chemical defense secreted from their abdomen (Lynch et al. 1980, Sorrells et al. 2011). Although they are numerically dominant throughout most of the growing season (Post and Jeanne 1982; B. T. Barton, *personal observation*), winter ants prefer relatively low temperatures, and consequently, are less active aboveground during the hottest parts of the day and year (Fellers 1989). Cornfield ants (*Lasius alienus*), in contrast, are generally subordinate to winter ants when exploiting the same food resource (Fellers 1987), but remain active throughout the summer growing season even at high temperatures (Post and Jeanne 1982, Fellers 1989). Thus, these two species compete for resources like honeydew, but their ability to exploit and defend these resources may be modulated by environmental conditions (Fellers 1987).

Average growing-season temperature at our study site is expected to increase 2.5°–4.5°C by 2055 (WICCI 2011). Because of the differences in thermal preference between winter ants and cornfield ants, increasing temperatures will likely affect the two species differently and have indirect effects on aphids by changing the strength of the ant–aphid mutualism. We tested this hypothesis in a series of field experiments aimed at understanding the interactive effects of warming, predators, and ants on corn leaf aphids. We predicted that warming would have a positive direct effect on aphid population growth rates, but that the net effect of warming on aphids would depend primarily on the indirect effects that involve predators and protection from the two ant mutualists.

MATERIALS AND METHODS

Field experiment

We conducted experiments at the University of Wisconsin Arlington Agricultural Research Station, Arlington, Wisconsin, USA, during the summer of 2011. Weather during the 2011 field season was typical for the location, with a mean daily temperature between 1 May and 1 October of 19°C (range 2.8°–30.0°C) and daytime maximum temperature often reaching >30°C (Appendix: Fig. A1). In late May, 2011, we established a field of sweet corn (0.20 ha; Green Giant code 63 cultivar) and allowed it to be colonized by corn leaf aphids and other arthropods. Fields were also naturally colonized by the two aphid-tending ants, *P. imparis* and *L. alienus* (identified by P. Pellitteri, Entomology, University of Wisconsin-Madison), which we refer to by the common names, winter ants and cornfield ants, respectively.

Our experimental design crossed three ant treatments (no ants, winter ants, or cornfield ants) with two predator treatments (with or without ladybeetles) and two temperature treatments (control or warmed), resulting in 12 treatment combinations that we replicated six times. On 5 September, we located 72 corn plants with corn leaf aphids being tended by either winter ants or cornfield ants (36 with each ant). We created "no ant" treatments by randomly selecting 12 plants with winter ants present and 12 plants with cornfield ants present, removing all ants, and applying a sticky barrier of Tanglefoot (Tanglefoot, Grand Rapids, Michigan, USA) to the base of the corn stalk to prevent ants and other arthropods from recolonizing. Creating "no ant" treatments from plants with ants controlled for any confounding factor that may have caused the absence of ants from a plant. Our previous surveys showed that average ladybeetle larval density in these cornfields was ~0.5 per plant (B. T. Barton and A. R. Ives, *unpublished data*), although their distribution is very heterogeneous. We maintained predator densities similar to our field observations by adding two ladybeetle third- or fourth-instar larvae collected from nearby fields to each plant each week. To maintain the appropriate combination of species in treatments, we enclosed each plant with a 200-cm tall fine-mesh bag (Spencer and Raghu 2009) that reached from the top of the plant to ~15 cm from the ground. Warming treatments were established by surrounding the plant and mesh bag with an open-top polyethylene cylinder (60 cm diameter × 1.5 m tall; Film-Gard, Minneapolis, Minnesota, USA) that elevated daily temperatures an average of 4.87° ± 0.14°C (mean ± SE; range 3.63°–5.90°C) above control plants. Although we did not measure humidity in this experiment, our experience with similar open-top designs found that warming chambers do not significantly affect humidity, and we saw no indication during this experiment that humidity differed between treatments (e.g., condensation inside the warming treatments or evidence of desiccation). At the initiation of the experiment (week 0) and every seven days thereafter, we counted all aphids and ants on the stalk, leaves, and tassels of each corn plant. Because aphids are sessile, these counts represent aphid population size. However, ants only visit plants to collect honeydew, and therefore,

these counts are an instantaneous index of ant activity-abundance.

Behavioral experiment

In the morning before each behavioral experiment, we collected third- and fourth-instar ladybeetle larvae from nearby fields. We then located colonies of aphids that were being tended by one of the two ant species near, but not within, the field experiment. Each behavioral trial was initiated by placing a ladybeetle within 5 cm of the aphid colony using a soft-bristled paintbrush. We recorded the time it took for an ant to make physical contact with the ladybeetle. If an ant had not made contact within 60 s, the trial was terminated. If any individual left the plant before contact (e.g., ladybeetle fell off the plant, or the ant left the colony), we abandoned the trial. At the end of each successful trial, we recorded the air temperature with a handheld electronic thermometer. These experiments were conducted midday between 12:00 and 16:00 hours to capitalize on natural variation in daily maximum temperature. We repeated this experiment three times each day for each species on eight days between 27 August and 26 September, 2011, for a total of 24 trials for each ant species.

Statistical analyses

We analyzed the aphid and ant abundance data using a repeated-measures linear mixed model (LMM; Littell et al. 2006, Gelman and Hill 2007, Qian and Shen 2007) with three treatment variables: warming (W), predation (P), and ant treatment (A). Specifically,

$$\log_{10}(\text{aphids}_i + 1) = W_i \times P_i \times A_i \times \text{time}_i + \varepsilon_{\text{rep}[i]} \quad (1)$$

where aphids$_i$ is the number of aphids in sample i, time is the week of the experiment treated as a categorical variable, and ×'s denote the inclusion of treatments and all of their interactions. The error $\varepsilon_{\text{rep}[i]}$ was assumed to have a AR(1) autocorrelation structure within replicates. To account for changes in the variance that is typical of count data, the variance of $\varepsilon_{\text{rep}[i]}$ was assumed to scale exponentially with the estimate of the mean; we used LMMs rather than traditional repeated-measures ANOVAs because they allowed the easy incorporation of this heteroscedasticity. We used a similar model to determine how ant abundance was affected by ant type (winter ants or cornfield ants), warming, and predator presence:

$$(\text{ants}_i)^{0.5} = W_i \times P_i \times A_i \times \text{time}_i + \varepsilon_{\text{rep}[i]}. \quad (2)$$

For the behavioral data, we first used a generalized linear mixed model (GLMM) to analyze how ant species and temperature affected whether or not there was an attack during the experiment:

$$\text{attack}_i = A_i + T_i + \text{date}_i \quad (3)$$

where date$_i$ is a random effect for the date of the experimental trial. We also used an LMM to determine how ant species and temperature affected how long (in seconds) it took for an attack to occur given that an attack did occur (i.e., the analysis included only trials in which an attack occurred within 60 s):

$$\text{responseTime}_i = A_i + T_i + \text{date}_i. \quad (4)$$

Finally, we partitioned the data set to include only trials with each ant species separately. All analyses were conducted using the nlme and car packages in the statistical computing language R (R Development Core Team 2010), and results are reported as type III sums of squares.

RESULTS

Field experiment

Our results show significant interactive effects of warming, ant, and predators treatments on aphid population growth ($\chi^2 = 22.2$, $N = 288$, $P = 0.0011$; Eq. 1; Fig. 1, Table 1). In the absence of ants and predators, warming had a positive direct effect on aphid population growth, increasing final aphid density after 21 days by $\sim50\%$ (Fig. 1a). However, the inclusion of predators reversed the positive direct effect of temperature so that aphid abundance in both control and warmed treatments declined (Fig. 1a).

The two ant species differed in their response to warming and their indirect effects on aphids when predators were present. Under control temperature treatments, winter ants had a strong positive effect on aphid population growth when predators were present, tripling the abundance of aphids relative to no ant treatments (Fig. 1b, Table 1). Under warming treatments, winter ant abundance decreased dramatically ($\chi^2 = 30.4$, $N = 192$, $P < 0.0001$; Eq. 2; Fig. 2; Appendix: Table A1) and, without protection from winter ants, aphid populations also declined (Fig. 1b, Table 1). In contrast, warming treatments increased the abundance of cornfield ants ($\chi^2 = 30.4$, $N = 192$, $P < 0.0001$; Eq. 2; Fig. 2; Appendix: Table A1). However, cornfield ants did not greatly benefit aphids under either temperature treatment, allowing predation to reduce aphid abundance (Fig. 1c).

Behavioral experiment

Winter ants were more aggressive toward intruding predators, attacking ladybeetle larvae in 80% of trials, compared to cornfield ants that only attacked during 25% of trials ($Z = 3.63$, $N = 48$, $P = 0.00028$; Eq. 3; Appendix: Table A2). When attacks were observed, winter ants attacked more rapidly (mean = 16.5 vs. 33.2 s for winter ants and cornfield ants, respectively; $t = 2.53$, $N = 25$, $P = 0.019$; Eq. 4; Appendix: Table A4). However, winter ants were slower to attack intruding ladybeetle larvae at higher temperatures ($t = 3.10$, $N = 19$, $P = 0.0065$; Eq. 4; Fig. 3a; Appendix: Table A5), whereas cornfield ants attacked predators similarly across all temperatures (Fig. 3b).
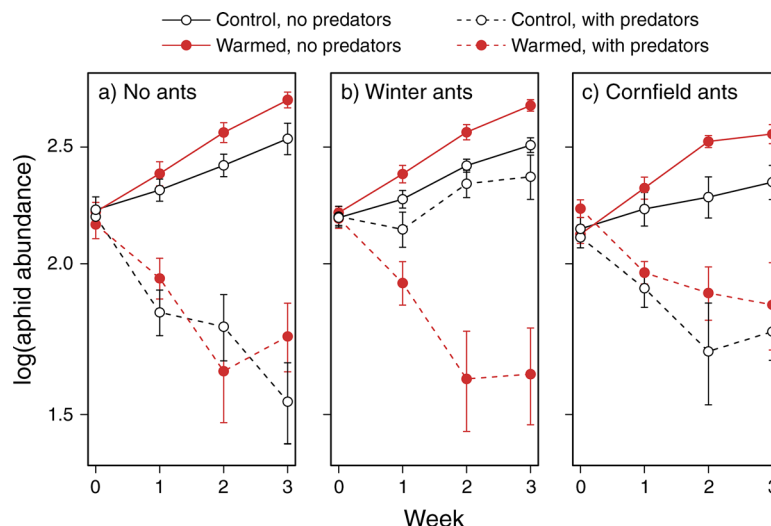
Reports

Fig. 1. The interactive effects of the predator Asian ladybeetle *Harmonia axyridis* (no predators shown with solid lines; with predators shown with dashed lines) and warming (control shown with open circles, warmed shown with solid red circles) on aphid (*Rhopalosiphum maidis*) abundance through time (*n* = 6) with (a) no ants, (b) winter ants (*Prenolepis imparis*), and (c) cornfield ants (*Lasius alienus*). Statistics are presented in Table 1.

DISCUSSION

Species exist within interconnected ecological communities, in which interactions between species can transmit the effects of an environmental perturbation throughout a community. Thus, the net effect of a perturbation on a species is a function of the direct effects and the indirect effects that arise via altered species interactions. Our results show this point: Despite having a positive direct effect on aphid population growth rate, the net effect of warming was to reduce aphid abundance. Although winter ants and cornfield ants both tend aphids, they were not perfectly functionally redundant. With the warming-induced decrease in winter ant abundance, cornfield ants assumed numerical dominance. However, cornfield ants did not mount the aggressive defense mustered by winter ants at control temperatures, leading to a reduction in corn leaf aphid population growth. Thus, the net effect of warming was to decrease aphid abundance by breaking down the ant–aphid mutualism and increasing predation.

Facultative mutualisms have long been known to be context dependent, existing only when the ratio of benefits to costs for each partner is high (Bronstein 1994, Sachs and Simms 2006). When the costs of engaging in a mutualistic interaction outweigh the benefits, species are expected to disengage from the mutualism, just as winter ants did when heat stressed in our experiment. The breakdown of a mutualism often has cascading effects as different sets of interactions change (Sachs and Simms 2006), as our experiments demonstrate. The first step in the cascade was to change winter ant behavior: Reduced aggression toward predators at higher temperatures allowed predation that reduced aphid abundance despite the higher potential population growth rates of the

aphids at high temperatures. The second step was the numerical loss of winter ants and subsequent replacement by cornfield ants. Thus, warming negatively affected winter ant function and abundance, and without the presence of a functionally redundant species, the mutualism broke down.

A limitation of our approach is that we did not measure the effects of warming on ant or ladybeetle demographics. In our experimental design, ants were able to leave the warmed plants and forage on plants that were not being warmed. In contrast, if the region's climate warms as expected, winter ants may not be able to leave warm plants in favor of cooler plants. They will

TABLE 1. Repeated-measures linear mixed model (LMM) showing the response of corn leaf aphid (*Rhopalosiphum maidis*) abundance to ant species, predator presence, and warming through time (Eq. 1).

Coefficient	df	χ^2	P
Ants	2	0.8	0.65
Predators	1	0.1	0.71
Warming	1	0.0	0.89
Time	3	39.1	<0.0001
Ants × predators	2	0.0	0.96
Ants × warming	2	0.1	0.94
Predators × warming	1	0.0	0.90
Ants × time	6	4.6	0.59
Predators × time	3	50.9	<0.0001
Warming × time	3	6.2	0.10
Ants × predators × warming	2	0.9	0.62
Ants × predators × time	6	29.3	<0.0001
Ants × warming × time	6	2.2	0.89
Predators × warming × time	3	7.8	0.050
Ants × predators × warming × time	6	22.2	0.0011

Notes: The autocorrelation among observations of the same replicate was $\rho = 0.57$, and the variance σ^2 proportional to the mean *m* according to exp(−0.62 *m*). *N* = 288 in 72 replicates (plants).
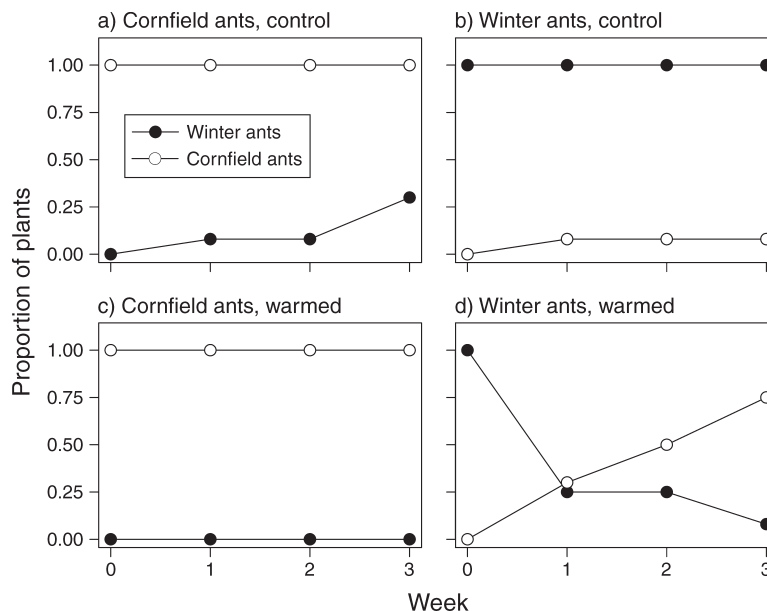
FIG. 2. Proportion of plants ($n = 6$) occupied by winter ants (solid circles) and cornfield ants (open circles) through time. On plants designated as cornfield ant treatments, cornfield ants were present throughout the experiment and were numerically dominant over winter ants in both (a) control and (c) warmed treatments. On plants designated as winter ant treatments, (b) winter ants were present throughout the experiment and numerically dominant over cornfield ants in control treatments, (d) but were replaced by cornfield ants in warmed treatments. Because both species could occupy the same plant at the same time, the summation of proportion of plants occupied by the two species can be >1.0. Statistics are presented in the Appendix: Table A1.

have to choose between not foraging at all (e.g., retreating to their belowground colonies) or foraging in a warmer environment. However, even if winter ants do the latter and continue to tend aphids, our behavioral experiments suggest that their aggression toward predators will decrease. Therefore, all evidence suggests that these aphids will be less protected in a warmer environment. We also did not measure the effect of warming on predators, and instead, used them as a treatment in our experimental design. This approach makes the assumption that warming will not change the abundance of predators and their predation rates. Although we did not measure this here, previous research suggests that warming can increase ladybeetle abundance and attack rate on herbivore pests (Lamana and Miller 1998, Soares et al. 2003). Therefore, our prediction that warming will negatively impact corn leaf aphids due to the indirect effects through predators and protection by mutualistic ants is likely to hold despite the limitations of our experiment.

Science and society focus on the negative impacts of climate change, and rightfully so. However, at least in this system, climate warming may have some benefit in terms of agricultural pest suppression. There is increasing concern about the effects of pesticides and conventional agricultural practices on ecosystems and human health, and a growing support for organic practices such as biological control of pests (Crowder et al. 2010). Although it was to the detriment of winter ants, warming indirectly reduced aphid abundance when

predators were present. Therefore, in our system and others where warming reduces the effectiveness of a mutualism involving an agricultural pest, the strengthened biological control of pests by natural enemies is a welcomed positive effect of climate change.
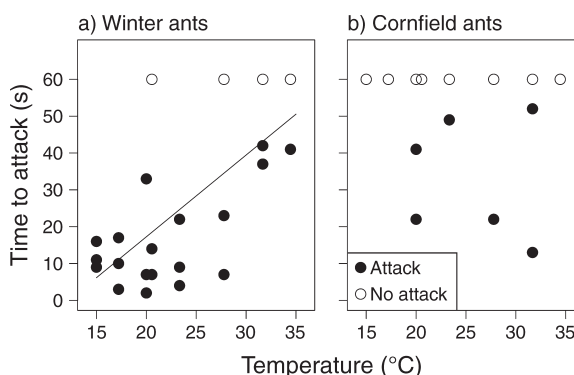

FIG. 3. Behavioral data of ants attacking ladybeetles giving the relationship between air temperature and time it took an aphid-tending ant to attack a ladybeetle larva placed near the aphid colony ($n = 24$). (a) Winter ants almost always attacked within 60 s, but attacked less quickly at higher temperatures. (b) During the few observed attacks by cornfield ants, there was no relationship between air temperature and time to attack. Solid circles denote observed attacks, and open circles denote no observed attack within 60 s. Statistics are presented in the Appendix: Tables A2–A5.

Reports

Literature Cited

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, and J. Farrar. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology 8:1–16.

Barton, B. T., and A. R. Ives. 2014. Species interactions and a chain of indirect effects driven by reduced precipitation. Ecology 95:486–494.

Bascompte, J., and D. B. Stouffer. 2009. The assembly and disassembly of ecological networks. Philosophical Transactions of the Royal Society B 364:1781–1787.

Breton, L. M., and J. F. Addicott. 1992. Density-dependent mutualism in an aphid–ant interaction. Ecology 73:2175–2180.

Bronstein, J. L. 1994. Conditional outcomes in mutualistic interactions. Trends in Ecology and Evolution 9:214–217.

Bronstein, J. L., U. Dieckmann, and R. Ferrière. 2004. Coevolutionary dynamics and the conservation of mutualisms. Pages 305–326 in R. Ferrière, U. Dieckmann, and D. Couvet, editors. Evolutionary Conservation Biology. Cambridge University Press, Cambridge, UK.

Carpenter, K. E., M. Abrar, G. Aeby, R. B. Aronson, S. Banks, A. Bruckner, A. Chiriboga, J. Cortes, J. C. Delbeek, and L. DeVantier. 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 321:560–563.

Crowder, D. W., T. D. Northfield, M. R. Strand, and W. E. Snyder. 2010. Organic agriculture promotes evenness and natural pest control. Nature 466:109–112.

El-Ibrashy, M., S. El-Ziady, and A. A. Riad. 1972. Laboratory studies on the biology of the corn leaf aphid, Rhopalosiphum maidis (Homoptera: Aphididae). Entomologia Experimentalis et Applicata 15:166–174.

Fellers, J. H. 1987. Interference and exploitation in a guild of woodland ants. Ecology 68:1466–1478.

Fellers, J. H. 1989. Daily and seasonal activity in woodland ants. Oecologia 78:69–76.

Foott, W. H. 1977. Biology of the corn leaf aphid, Rhopalosiphum maidis (Homoptera: Aphididae), in southwestern Ontario. Canadian Entomologist 109:1129–1135.

Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge, UK.

Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt. 2010. A framework for community interactions under climate change. Trends in Ecology and Evolution 25:325–331.

Gray, H. E., and G. Fraenkel. 1954. The carbohydrate components of honeydew. Physiological Zoology 27:56–65.

Kiers, E. T., T. M. Palmer, A. R. Ives, J. F. Bruno, and J. L. Bronstein. 2010. Mutualisms in a changing world: an evolutionary perspective. Ecology Letters 13:1459–1474.

Lamana, M. L., and J. C. Miller. 1998. Temperature-dependent development in an Oregon population of Harmonia axyridis (Coleoptera: Coccinellidae). Environmental Entomology 27:1001–1005.

Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 2006. SAS system for mixed models. Second edition. SAS Institute, Cary, North Carolina, USA.

Lynch, J. F., E. C. Balinsky, and S. G. Vail. 1980. Foraging patterns in three sympatric forest ant species, Prenolepis imparis, Paratrechina melanderi and Aphaenogaster rudis (Hymenoptera: Formicidae). Ecological Entomology 5:353–371.

Marquis, M., I. Del Toro, and S. L. Pelini. 2013. Insect mutualisms buffer warming effects on multiple trophic levels. Ecology 95:9–13.

Post, D. C., and R. L. Jeanne. 1982. Rate of exploitation of arboreal baits by ants in an old-field habitat in Wisconsin. American Midland Naturalist 1081:88–95.

Qian, S. S., and Z. Shen. 2007. Ecological applications of multilevel analysis of variance. Ecology 88:2489–2495.

R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rosenfeld, J. S. 2002. Functional redundancy in ecology and conservation. Oikos 98:156–162.

Sachs, J. L., and E. L. Simms. 2006. Pathways to mutualism breakdown. Trends in Ecology and Evolution 21:585–592.

Sakata, H. 1995. Density-dependent predation of the ant Lasius niger (Hymenoptera: Formicidae) on two attended aphids Lachnus tropicalis and Myzocallis kuricola (Homoptera: Aphidiidae). Researches on Population Ecology 37:159–164.

Soares, A. O., D. Coderre, and H. Schanderl. 2003. Effect of temperature and intraspecific allometry on predation by two phenotypes of Harmonia axyridis Pallas (Coleoptera: Coccinellidae). Environmental Entomology 32:939–944.

Sorrells, T. R., L. Y. Kuritzky, P. G. Kauhanen, K. Fitzgerald, S. J. Sturgis, J. Chen, C. A. Dijamco, K. N. Basurto, and D. M. Gordon. 2011. Chemical defense by the native winter ant (Prenolepis imparis) against the invasive Argentine ant (Linepithema humile). PLoS ONE 6:e18717.

Spencer, J. L., and S. Raghu. 2009. Refuge or reservoir? The potential impacts of the biofuel crop Miscanthus giganteus on a major pest of maize. PLoS ONE 4:e8336.

Stachowicz, J. J. 2001. Mutualism, facilitation, and the structure of ecological communities: Positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on which many species depend. Bioscience 51:235–246.

Stirling, I., and A. E. Derocher. 2012. Effects of climate warming on polar bears: a review of the evidence. Global Change Biology 18:2694–2706.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11:1351–1363.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Way, M. J. 1963. Mutualism between ants and honeydew-producing Homoptera. Annual Review of Entomology 8:307–344.

WICCI [Wisconsin Initiative on Climate Change Impacts]. 2011. Wisconsin's changing climate: impacts and adaptation. Nelson Institute for Environmental Studies, University of Wisconsin-Madison and the Wisconsin Department of Natural Resources, Madison, Wisconsin, USA.

Supplemental Material

Appendix

Statistical results and daily temperature data from the field site (*Ecological Archives* E095-131-A1).