

# Species interactions and a chain of indirect effects driven by reduced precipitation

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**Abstract.** Climate change can affect species directly and indirectly by altering interactions between species within communities. These indirect effects can ramify through a community and affect many species, including some that may not have been directly affected by the perturbation. Identifying these chains of indirect effects is difficult, and most studies only follow indirect effects across two or three species. Here, we use a factorial field experiment to demonstrate that precipitation affects spotted aphids through a complex chain of indirect interactions that are mediated by other herbivores and a generalist predator. We experimentally simulated drought, which reduced water content in alfalfa plants. While water stress in alfalfa had no direct effect on spotted aphids, it lowered the population growth rate of pea aphids, another common alfalfa pest. Because ladybeetle predators were attracted to high pea aphid densities, predator densities were lower in drought treatments. Consequently, spotted aphid densities were released from top-down control (apparent competition) in drought treatments and reached densities three times higher than spotted aphids in ambient treatments with high pea aphid densities. Thus, drought affected spotted aphids in the interaction chain: drought → alfalfa → pea aphids → predators → spotted aphids. This result illustrates the lengthy path that indirect effects of climate change may take through a community, as well as the importance of community-level experiments in determining the net effect of climate change.

**Key words:** alfalfa, *Medicago sativa*; apparent competition; biocontrol; climate change; drought; ladybeetles; mesocosm field experiment, Madison, Wisconsin, USA; pea aphid, *Acyrtosiphon pisum*; precipitation; predator–prey interactions; spotted aphid, *Therioaphis maculata*; top-down control.

## INTRODUCTION

Ecological communities are often complex and highly reticulate, with each species being directly or indirectly connected to all other species in the community (Wootton 1994). Thus, when one species is affected directly by an environmental perturbation such as those associated with climate change, the perturbation can be propagated throughout the community (Walther et al. 2002, Emmerson et al. 2004, Tylianakis et al. 2008). These indirect effects can be driven either by changes in the abundances of species (e.g., a prey species experiences higher mortality at higher temperature and as a result of its lower abundance, the population of a predator starts to decrease) or by changes in the strength of interactions between them (Wootton 1994). Because multiple species will likely be simultaneously affected by climate change directly, there will be multiple pathways of indirect effects propagated through a community. Therefore tracing chains of indirect interactions and anticipating the ultimate outcome of climate change for a community is difficult.

In previous studies the importance of species interactions and indirect effects for community responses to environmental change has mainly been investigated using one of three approaches. The first focuses on only interactions between two species, such as how climate influences specific plant–herbivore (Newman 2003, Post and Pedersen 2008), predator–prey (Joern et al. 2006, Harmon et al. 2009), or plant–pollinator interactions (Rafferty and Ives 2012). This approach has been useful to demonstrate that species interactions can transmit indirect effects of environmental change, but is limited in its inference about the ramifying effects that could propagate throughout an interconnected community.

A second approach has been to examine the unidirectional effects of climate change through a linear, tri-trophic food web. These studies typically examine how an abiotic manipulation moves upward from primary producers to predators (Bezemer et al. 1998, Hoover and Newman 2004, Warne et al. 2010), or downward from predators to primary producers (Chase 1996, Barton 2010, Wu et al. 2010). Although ecology has a long history of categorizing ecological systems as being either bottom-up or top-down, these two pathways are not mutually exclusive. Emphasizing a unidirectional flow of effects from climate change ignores the possibility of bidirectional effects: bottom-

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up effects that reach top predators may initiate top-down effects, or vice versa.

A third, whole-community approach examines changes in abundances of all species, or species aggregated into functional groups, within a community simultaneously (Paine 1974, Bender et al. 1984, Wootton 1994, Ives et al. 1999, Hampton et al. 2008). In most studies using this approach the abundance or presence of a species was manipulated, rather than an environmental variable, although the approach could be applied equally in either case. However, this statistical approach makes it difficult to test specific a priori hypotheses about how an environmental perturbation may affect a particular food web embedded in a larger community.

In this paper we trace the indirect effects of drought upward and then downward through a simple agricultural community. Pea aphids (*Acyrtosiphon pisum*) and spotted aphids (*Therioaphis maculata*) are two common pests in the alfalfa (lucerne, *Medicago sativa*) fields of Wisconsin, USA, yet they are affected by drought differently. Previous work showed that pea aphid population growth rates are strongly tied to alfalfa water content, reaching high densities in healthy alfalfa but suffering lower growth rates when alfalfa is water stressed (Forbes et al. 2005). In contrast, spotted aphids are insensitive across a wide range of alfalfa moisture levels and are seemingly unaffected by precipitation. Competition between pea aphid and spotted aphids is weak (Forbes et al. 2005), but because they share a suite of natural enemies, predators could mediate interactions between these two aphids. One of the most common predators of pea and spotted aphids is the multicolored Asian ladybeetle (*Harmonia axyridis*). As adults these ladybeetles are highly mobile, and preferentially seek out locations with high pea aphid abundance (Osawa 2000, Forbes and Gratton 2011).

We predicted that decreased precipitation (simulated drought) would have a negative effect on alfalfa water content, inhibiting pea aphid populations from reaching high densities that attract ladybeetle predators. In the absence of high pea aphid densities and the ladybeetles they attract, predation on spotted aphids would decrease and their densities would increase. Therefore, we predicted that precipitation would indirectly increase the density of spotted aphids through a chain of interactions with four links: drought → alfalfa → pea aphids → ladybeetles → spotted aphids. Although different species could be affected by precipitation changes through multiple pathways (Shipp et al. 2003, Ovadia and Schmitz 2004, Aslam et al. 2013), our approach was to follow the indirect effects initiated by the response of a single species (alfalfa) through as many links in a food web as feasible. This illustrates how far a single indirect effect can propagate through a food web and emphasizes the ability of species interactions to generate indirect effects throughout a community.

## MATERIALS AND METHODS

We conducted a factorial experiment at the University of Wisconsin–Madison Arlington Agricultural Research Station (Madison, Wisconsin, USA) during the summer of 2010 to examine the effects of reduced precipitation on species interactions in alfalfa communities. Specific projections of future precipitation for this region during the summer growing season vary greatly among climate models (WICCI 2011). In general, during the next 100 years total summer precipitation will increase little if at all, but the timing and magnitude of precipitation events will change. Projections for year 2100 suggest storms depositing 10 mm or more of rain in 24 h will increase by  $\sim 7\% \pm 13\%$  (mean  $\pm$  SD), but the frequency of precipitation events will decrease (WICCI 2011) and the number of consecutive days without precipitation will increase 15% (WICCI 2011, CCCSN 2012). Coupled with increased evapotranspiration associated with a 2.5–5°C increase in mean temperature, Wisconsin is likely to experience an increase in short-term droughts during the summer growing season (WICCI 2011).

Our experimental design crossed two precipitation treatments (ambient and drought) with three aphid-species treatments (pea aphids only, spotted aphids only, or both species). We constructed 30 mesocosms from wooden frames approximately  $1 \times 1 \times 1$  m. These frames were assembled over alfalfa growing in a production field where alfalfa stem density was  $\sim 200$ – $300$  stems/m<sup>2</sup> (Fig. 1). Mesocosms were arranged in two rows of 15 and spaced 3–4 m apart. The top of each mesocosm was covered in clear 4-mm plastic sheeting (Film-Guard, Minneapolis, Minnesota, USA) and sloped  $\sim 5^\circ$  from horizontal. We attached a plastic rain gutter with corrugated plastic pipe to the lowest edge of each mesocosm, which collected and diverted rainwater either into (ambient treatments) or outside (drought treatments) each mesocosm. Finally, insect netting was wrapped around each frame and secured with removable clips.

We took two additional steps to ensure soil moisture was reduced in our drought treatments. First, we conducted our experiment in an alfalfa stand that was less than one year old. Older alfalfa plants develop substantial root systems that can access soil moisture far below the surface, and thus may not be affected by our small-scale precipitation treatments. Second, we encircled each mesocosm with a moisture barrier; 50 cm from each mesocosm we buried plastic sheeting to a depth of 15–25 cm.

To confirm that the simulated drought treatment affected alfalfa water content, we measured leaflet water content three times during the experiment (beginning, middle, and end). We removed three randomly selected alfalfa leaflets from each mesocosm. Samples were immediately transported to the laboratory where their fresh mass ( $M_f$ ) was recorded. Samples were then soaked in water for 12 h and reweighed to determine their saturated mass ( $M_s$ ). Finally, each sample was

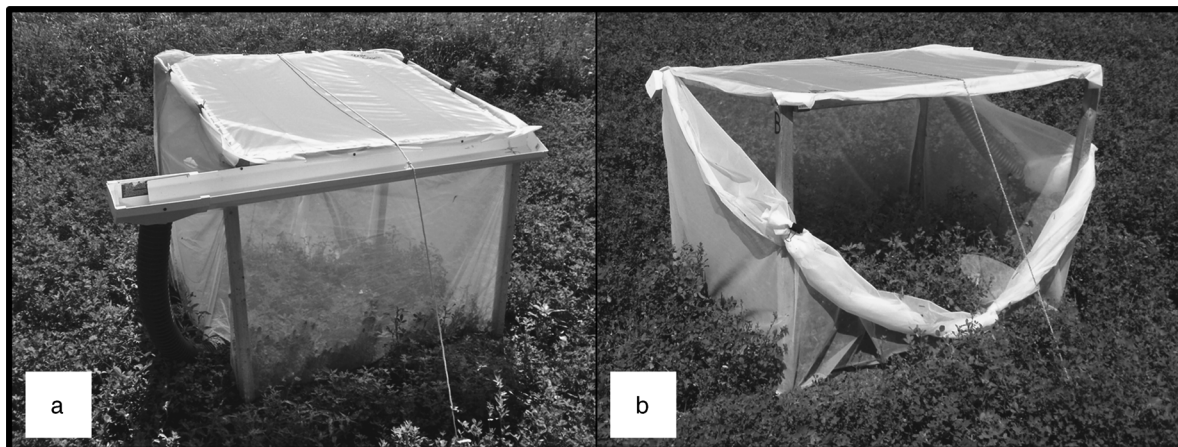


FIG. 1. Photographs of mesocosms used during the field experiment in Madison, Wisconsin, USA. Plastic tops and rain gutters manipulated precipitation within mesocosms to maintain either ambient or drought treatments, and predator access was manipulated by (a) closing or (b) opening the mesh surrounding each mesocosm. Dimensions are approximately  $1 \times 1 \times 1$  m. The photo was taken by B. T. Barton in 2010 at Arlington Agricultural Experiment Station in Madison, Wisconsin, USA.

dried in a drying oven for 48 h and again weighed to determine its dry mass ( $M_d$ ). Using these masses we calculated relative water content (RWC; González and González-Vilar 2001) as  $RWC = (M_f - M_d)/(M_s - M_d) \times 100$ .

Precipitation treatments were initiated on 28–29 July 2010. On 9 August 2010 we simulated alfalfa harvest that occurs within production fields by cutting the alfalfa around and within all mesocosms to a height of  $\sim 15$  cm. Two days later we removed all visible arthropods and we stocked mesocosms with aphids. To maintain similar aphid biomass among species treatments, we stocked pea aphids (which are larger than spotted aphids) at 20 aphids/mesocosm and spotted aphids at 50 aphids/mesocosm; the treatment with both species received 10 pea and 25 spotted aphids.

After allowing two days for the aphids to establish on the alfalfa, we sampled three times weekly (Monday, Wednesday, and Friday) by examining 100 alfalfa stems per mesocosm ( $\sim 20$ – $30\%$  of total stems) and recording pea aphid, spotted aphid, and predator density. Mesocosms were fully enclosed by mesh to exclude predators for the first five sampling events (Fig. 1a). After sampling aphids on day 11 we opened the mesocosm on three sides and allowed predator colonization during the last five sampling events (Fig. 1b). Although screening was removed, dispersal of pea and spotted aphids from the mesocosm was limited; wingless aphids are generally sedentary, and we saw no winged adults arise during the experiment, presumably because populations never reached the extremely high densities that prompt wing development. This experimental design and the duration of the study (21 d) emphasized the role of predator immigration over predator reproduction. In our system this is an appropriate emphasis, because ladybeetle predators (in particular *Harmonia axyridis*) are very mobile generalist predators, and their popula-

tion dynamics are not expected to be strongly tied to the abundance of aphids in a single alfalfa field (Osawa 2000, Snyder and Ives 2003, Forbes and Gratton 2011).

The average temperature during the 21-d experiment was  $23^\circ\text{C}$  (range,  $15$ – $33^\circ\text{C}$ ). Precipitation occurred on six days resulting in a cumulative rainfall of 88 mm. The control plots were exposed to this precipitation, while the drought-treatment plots received no water. Therefore, our drought treatments were effectively  $-88$  mm of precipitation relative to the control treatments during 21 days. This magnitude of drought is on the extreme side of predictions from climate models, approximately 4–5 times stronger than the average expected drought and 25% stronger than the most extreme predictions in the SR-A2 scenario (IPCC 2007; J. Newman, *personal communication*). Nonetheless, this perturbation allowed us to statistically detect treatment effects with a reasonable sample size.

#### Statistical analyses

We analyzed the RWC of alfalfa using a linear mixed model (LMM) to account for repeated measures from the same mesocosms at the beginning (12 August), middle (23 August), and end (3 September) of the experiment. We examined the main and interactive effects of precipitation treatment (control or drought), aphid treatment (pea aphid, spotted aphid, or both species), and time on alfalfa RWC.

We also used LMM to analyze the arthropod abundance data to account for repeated measures. The aim of the experiment was to determine the effects on aphid population growth of the drought treatment, the presence/absence of the other aphid species, and whether predators were excluded or allowed to attack aphids. Thus, there are three treatment variables: drought ( $D$ ), presence of heterospecific aphids ( $H$ ), and predation



(*P*). For the abundance of each species (spotted or pea aphids), we fit the following model:

$$\log_{10}(\text{aphids} + 1) = D_i \times H_i \times P_i \times \text{time}_i + e_{\text{rep}[i]} \quad (1)$$

where  $\text{aphids}_i$  is the number of individuals counted in sample  $i$ , asterisks denote the inclusion of treatments and all of their interactions, and the function  $\text{rep}[i]$  maps the sample record  $i$  onto the replicate. Because we are particularly interested in the experimental period during which predators were present, we coded  $P$  (predation) as 1, absent and 0, present = 0, so that the period with predators present occurred in the absence of the  $P$  interaction terms; this simplifies the interpretation of the interactions. The other treatments were coded  $D = 0$  (Control) or 1 (Drought), and  $H = 0$  (single species) or 1 (with the other species). The predictor variable  $\text{time}$  is the day of the experiment. Although time is treated as a categorical variable in a traditional repeated-measures design, here we treat  $\log(\text{aphid abundance})$  as a linear function of time over the periods when predators are excluded and when predators are allowed; this is equivalent to the assumption that aphid populations are growing or declining exponentially. At low aphid population density the population counts were variable due to measurement error. Therefore, we weighted the variances of the residuals by assuming the variance was an exponential function of the predicted values, estimating the parameter of the exponential function during the model fitting. To account for autocorrelation in the residuals, we assumed that the residuals  $e_{\text{rep}[i]}$  taken from consecutive measurements in the same replicate (mesocosm) have autocorrelation coefficient  $\rho$ . This statistical design is the same as that discussed and justified in Ives and Zhu (2006). We used backwards-stepwise regression to reduce the model to contain only terms that were statistically different from zero at the  $\alpha = 0.05$  level. For comparisons among models that differed by more than one parameter, we used a likelihood ratio test (LRT) rather than a standard  $F$  test, because we have found this is more conservative (more likely to give a larger  $P$  value). The analysis was performed using the nlme package in the statistical computing language R (R Development Core Team 2010).

Even though we are interested in the changes in aphid populations in the two separate phases of the experiment (with and without predator exclusion), we analyzed the data from the entire experiment simultaneously. Simulations based on our data set showed that analyzing the entire data set resulted in greater statistical power than analyzing the first and second phases of the experiment separately. Analyzing the entire data set gives a better characterization of the variance components of the model and reduces confounding effects among the interaction terms.

We analyzed the predator response to treatments using a generalized linear mixed model (GLMM) in which the distribution of ladybeetles was modeled as a

Poisson-lognormal process; this accounts for the variability in the response variable, especially numerous zeros, due to the count nature of the data:

$$\Pr(Y_i = n) \sim \text{Poisson}(L_i)$$

$$L_i = \exp(D_i \times S_i + \text{sample}_i + a_{\text{rep}[i]} + e_i) \quad (2)$$

where  $S_i$  is the aphid species treatment (spotted aphids, pea aphids, or both), and  $\text{sample}_i$  is a categorical variable (factor) for the day of the sample; the asterisk denotes the inclusion of treatments  $D$  and  $S$ , and their interaction. The random effect  $a_{\text{rep}[i]}$  is a Gaussian random variable that takes the same value for each observation in a replicate; thus,  $a_{\text{rep}[i]}$  accounts for repeated observations from the same replicate (mesocosm). Finally, the individual-level random effect  $e_i$  accounts for possible overdispersion (Elston et al. 2001, Bolker et al. 2009). We treated time as a categorical variable using  $\text{sample}_i$  rather than as a continuous variable  $\text{time}_i$  (Eq. 1), because predators are mobile and likely to arrive and leave replicates on a time scale shorter than the interval between samples. This contrasts with our analysis of aphid population dynamics, in which increases and decreases in populations within replicates were mainly the result of reproduction and mortality. We used backward-stepwise regression to reduce the model, although we did not remove  $\text{sample}_i$  so that possible time dependence of the results was retained. For statistical tests, we performed parametric bootstrapping using 2000 simulations; if no simulated data set gave a parameter estimate that violated the null hypothesis, then we report  $P < 0.01$  and also performed a likelihood ratio test. This analysis was performed using the lme4 package in the statistical computing language R (R Development Core Team 2010).

Using a similar model, we also compared the number of predators under ambient (Control) precipitation between the case with only spotted aphids and the case with spotted and pea aphids. This model had the same structure as Eq. 2, although it did not include  $D_i$ .

## RESULTS

### *Alfalfa relative water content*

Alfalfa leaf relative water content (RWC) in Drought treatments was 10–13% less than in Control treatments. This effect of precipitation treatment (ambient or drought) was significant (LMM,  $F_{1,26} = 27.250$ ,  $P < 0.0001$ ), but there was no precipitation treatment  $\times$  time interaction ( $P = 0.153$ ). There was also no significant effect of aphid treatment ( $P = 0.657$ ) or aphid treatment  $\times$  time interaction ( $P = 0.510$ ) on RWC.

### *Aphid densities*

Both aphid species showed similar responses to the treatments, with the exception that spotted aphids showed  $H$  (heterospecific aphids)  $\times D$  (drought) and  $H \times D \times \text{time}$  interactions whereas pea aphids did not (Fig. 2; see Appendix: Table A1 for a summary table of

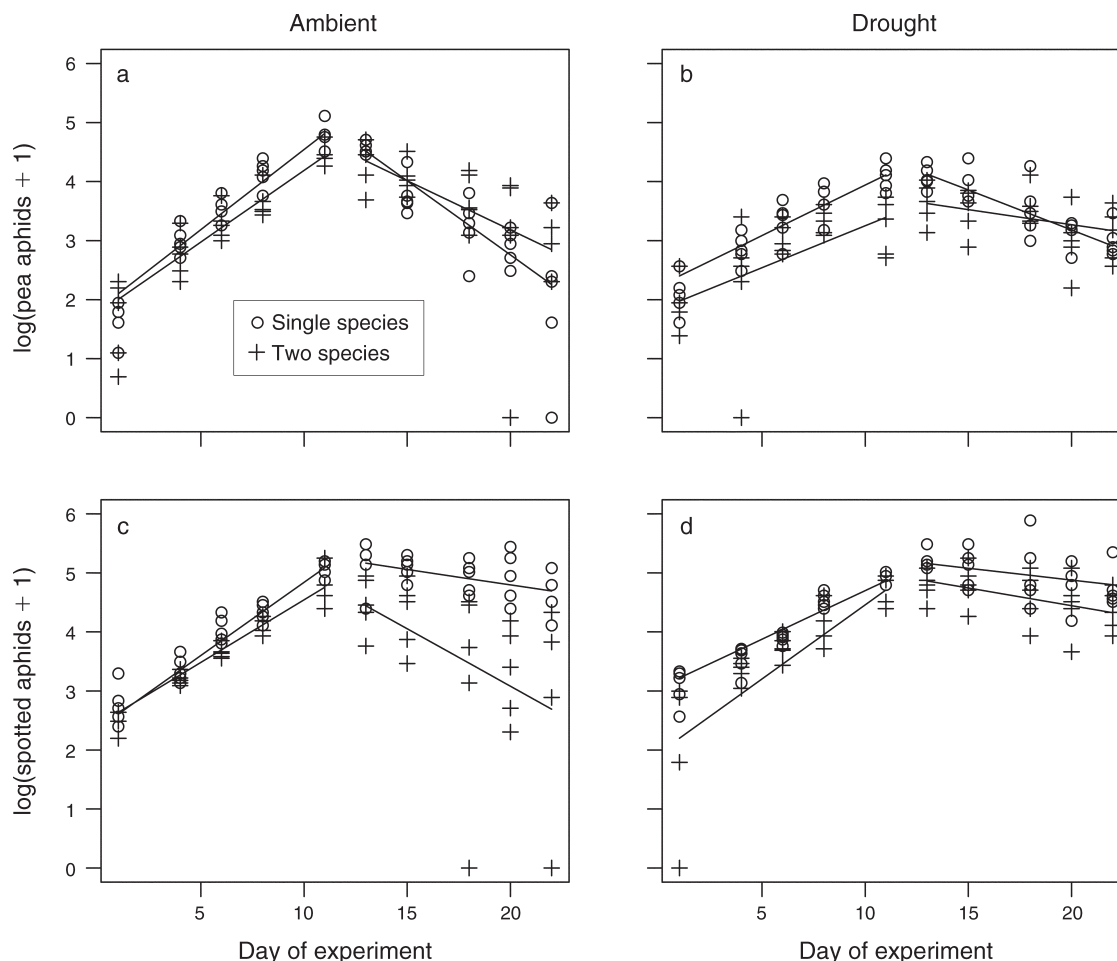


FIG. 2. Interactive effects of simulated drought, aphid species composition (single species or in the presence of a heterospecific), and predation on (top panels) pea aphid (*Acyrtosiphon pisum*) and (bottom panels) spotted aphid (*Therioaphis maculata*) abundance in 30 mesocosms (see Appendix). Predators were excluded during the first 10 days of the experiment and allowed to colonize mesocosms after sampling on day 11.

results). These interactions mean that in the presence of predators and in the presence of pea aphids, spotted aphids showed a more rapid decline in log density in the Control treatment (ambient precipitation) than in the Drought treatment. In the treatments with both aphid species, immediately before exposure to predators (day 11) pea aphids were more common in the Control treatment than in the Drought treatment ( $t_1 = -5.14$ ,  $P = 0.0009$ ), suggesting that the more rapid decrease in spotted aphids in the Control treatment could have been the indirect result of higher pea aphid densities.

To compare the results for spotted vs. pea aphids we applied the best-fitting model for the pea aphid data to the spotted aphid data. Specifically, we removed the  $H \times D$  and  $H \times D \times \text{time}$  interactions from the spotted aphid model (Appendix). The fit of the reduced model to the spotted aphid data was much worse than the best-fitting model (LMM LRT,  $\chi^2_2 = 55.6$ ,  $P \ll 0.0001$ ), implying that the interaction between Drought and the presence of pea aphids strongly affected spotted aphid dynamics.

Reversing the roles of spotted and pea aphids by applying the best-fitting spotted aphid model (including  $H \times D$  and  $H \times D \times \text{time}$ ) to pea aphid data showed no significant interaction between Drought and the presence of spotted aphids (LRT,  $\chi^2_2 = 3.91$ ,  $P = 0.14$ ).

#### Predator densities

We detected no predators within mesocosms during the first 10 days of the experiment, when the insect netting around mesocosms was closed. After the insect netting was removed, we detected only adult *Harmonia axyridis* ladybeetles, as the experiment was terminated before predator reproduction could occur. Predator numbers were higher in treatments with pea aphids than those with only spotted aphids (GLMM parametric bootstrapping,  $P < 0.01$ , LRT,  $\chi^2_2 = 17.5$ ,  $P < 0.0002$ ; Fig. 3); furthermore, predator numbers were higher in the Control treatment than the Drought treatment (GLMM, parametric bootstrapping,  $P = 0.021$ ). There was no interaction between precipitation treatment and

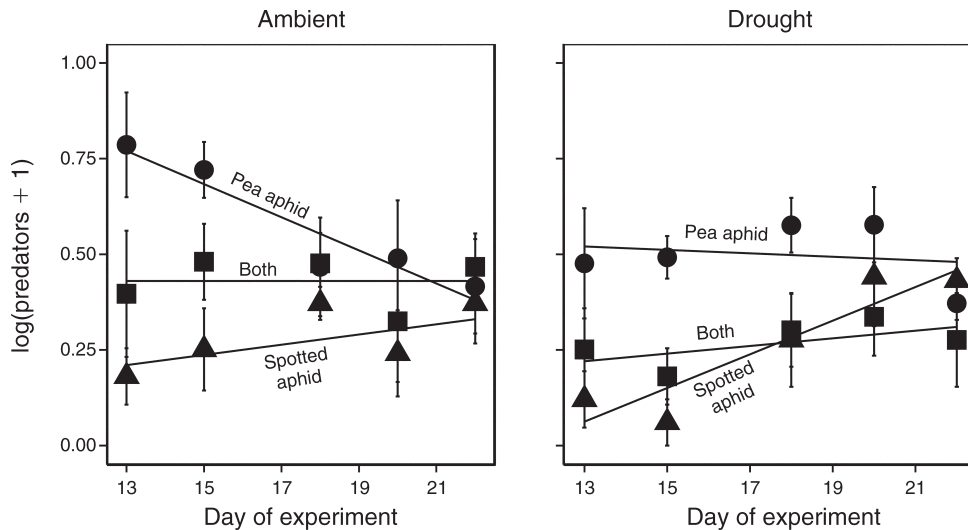


FIG. 3. Interactive effects of simulated drought and aphid community composition on predator abundance in 30 mesocosms. Mesocosms were opened on day 11 of the experiment to allow predator colonization. Predator abundance data are log-transformed means  $\pm$  SD. Markers and error represent mean predator abundance  $\pm$  standard deviation, and shapes distinguish aphid community composition treatments (circles, pea aphids only; triangles, spotted aphids only; squares, both species together).

aphid treatment,  $D \times S$  (GLMM parametric bootstrapping  $P=0.20$ ) implying that the Drought treatment reduced the predator abundance the same amount (on a log scale) for pea aphids alone, pea and spotted aphids, and spotted aphids alone. In the key comparison between the treatments with spotted aphids alone vs. treatments with both spotted and pea aphids under ambient (Control) precipitation, there were indeed more predators in the presence of pea aphids than when spotted aphids were alone (GLMM, parametric bootstrapping  $P=0.016$ ; Fig. 3).

#### DISCUSSION

Climate change can affect species both directly and indirectly by altering interactions with other members of their community. When ecologists focus only on direct effects, they risk misunderstanding the total effect of climate change on species and their communities, especially because indirect effects will likely follow many pathways through reticulated food webs. Here, in a factorial mesocosm field experiment in Madison, Wisconsin, USA, we showed that complex species interactions transmit the indirect effects of short-term drought across four species in a simple agroecosystem.

Simulated drought had a direct effect on alfalfa, as shown by reduced relative water content of alfalfa leaves. Although not investigated here, drought treatments may have altered phloem nutrients (Johnson et al. 2011, Aslam et al. 2013), which is a likely mechanism explaining the reduced population growth rate of pea aphids observed in drought treatments. Because colonization of mesocosms by ladybeetles was positively related to pea aphid density, the decrease in pea aphid abundance caused by drought reduced the predation rate on co-occurring spotted aphids. Thus, even though

spotted aphids were not directly affected by alfalfa moisture content, spotted aphids abundance increased significantly in the drought treatments because they experienced reduced predation.

An alternative hypothesis for greater spotted aphid density in the drought treatments is that competitive release from fewer pea aphids could lead to higher reproduction, lower mortality or less dispersal. This explanation, however, is not consistent with the evidence. The populations of both pea and spotted aphids were increasing exponentially before predator exclosures were removed, and densities of spotted aphids in all treatments were the same when the mesocosms were opened (after accounting for different initial stocking densities between single- and both-species treatments). This argues against density-dependent reproduction or mortality. Although not quantified here, dispersal of spotted aphids was likely very low after mesocosm screens were removed, because non-winged spotted aphids are sedentary, and we saw no production of winged adults. Thus, the positive effect of drought on spotted aphid abundance when pea aphids were present is best explained by the low abundance of pea aphids attracting fewer predators.

Our results highlight three broad issues about how climate change can affect communities. First, species that are not directly affected by climate change may nonetheless be indirectly affected. For example, our spotted-aphid-only treatments show that precipitation has relatively little direct influence on spotted aphid densities. This is true even though the magnitude of our simulated drought was extreme, 4–5 times greater than the average 21-day drought in Wisconsin's predicted future climate regime (J. Newman, *personal communication*). However, when the effects of precipitation on



PLATE 1. Asian ladybeetle (*Harmonia axyridis*) eating a pea aphid (*Acyrtosiphon pisum*). Photo credit: A. R. Ives.

spotted aphids were considered within a broader community-level context, reducing precipitation increased spotted aphid density by reducing apparent competition. Many studies have reported climate effects that only manifest at the food web or community level, suggesting the net effects of climate change can easily be missed if species interactions are ignored. For example, Johnson et al. (2011) showed that drought had little effect on the abundance of bird cherry–oat aphids (*Rhopalosiphum padi*) when earthworms (*Aporrectodea caliginosa*) were excluded. However, when earthworms were included in the community, drought treatments decreased aphid abundance by as much as 80%, probably because earthworms reduce soil water-storage capacity and negatively affect cellular plant processes (Blouin et al. 2007, Johnson et al. 2011). Similarly, Barton et al. (2009) showed that warming did not influence a grassland plant community when plants were examined alone or with grasshopper (*Melanoplus femurrubrum*) herbivores present. Instead, warming only affected plants in the presence of grasshoppers and spiders (*Pisaurina mira*), because warming altered spider behavior and increased the strength of top-down control (Barton 2010). Finally, Greig et al. (2012) demonstrated that the presence of predatory fish could exacerbate or ameliorate the effects of warming and eutrophication on many components of an aquatic ecosystem, including insect and amphibian emergence, plant decay rates, and consumer biomass. Experiments like these demonstrate

the importance of top predators, competitors, and detritivores in driving indirect effects of climate change in diverse study systems.

Second, climate change may affect communities simultaneously via bottom-up and top-down processes. Few studies explicitly trace both bottom-up and top-down effects through a community, leaving a gap in our understanding of how the relative strengths of these two processes will change in the future. This is especially true for the effects of precipitation, where the bulk of research has focused on plant responses and consequent bottom-up effects on consumers (Bakkenes et al. 2002, Knapp et al. 2002, Weltzin et al. 2003, Zavaleta et al. 2003). However, upon reaching higher trophic levels, these bottom-up effects can cascade back down a food web and have important top-down effects (Suttle et al. 2007). Therefore, bottom-up and top-down processes are not independent, but influence one another in complex ways. Is this bidirectional flow of effects through a community common in nature? Do bottom-up effects of climate change commonly cascade back down from predators to prey? Do top-down effects alter plant communities or productivity? Resolving the interactive effects of bottom-up and top-down processes is essential to understand the net effects of climate change on communities (Merve et al. 2003, Wilmers et al. 2006).

Third, while the goal of predicting the net effect of changing climate on multi-trophic communities may



often be difficult (Harrington et al. 1999, Newman 2003, Pritchard et al. 2007), it is not impossible. We successfully generated a priori qualitative predictions about the effects that reduced precipitation would have on our system by synthesizing available information on these species. This was possible because of previous work asking basic questions about the effects of precipitation on these two aphid species (Forbes et al. 2005) as well as the general ecology of the community (Snyder and Ives 2003, Harmon et al. 2009). Thus, predicting the net effect of climate change on communities will likely benefit from basic research into the functioning of ecological systems.

We have investigated the indirect effects of a single environmental perturbation on a community of interacting plants and arthropods, and shown that a single direct effect can generate far-reaching effects within a community. We recognize that this is a relatively simple system, involving four species and only a single direct effect (on alfalfa). This simplicity allowed us to single out the chain of indirect effects generated by altered precipitation. However, in communities in which multiple species experience direct effects of environmental perturbations, we would expect multiple chains to emerge, intertwine, and interact. Consequently, for many communities and climatic perturbations, dissecting out a single chain of indirect effects will be more challenging than in our study system. Nonetheless, the ecological importance of cascading indirect effects means that this challenge must be taken up.

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#### SUPPLEMENTARY MATERIAL

##### Appendix

A table of results from the linear mixed model ([Ecological Archives E095-043-A1](#)).