

LETTER

Experimental warming transforms multiple predator effects in a grassland food web

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Abstract

This experimental study tests new theory for multiple predator effects on communities by using warming to alter predator habitat use and hence direct and indirect interactions in a grassland food web containing two dominant spider predator species, a dominant grasshopper herbivore and grass and herb plants. Experimental warming further offers insight into how climate change might alter direct and indirect effects. Under ambient environmental conditions, spiders used habitat in spatially complementary locations. Consistent with predictions, the multiple predator effect on grasshoppers and on plants was the average of the individual predator effects. Warming strengthened the single predator effects. It also caused the spider species to overlap lower in the vegetation canopy. Consistent with predictions, the system was transformed into an intraguild predation system with the consequent extinction of one spider species. The results portend climate caused loss of predator diversity with important consequences for food web structure and function.

Keywords

Cascading effects, climate warming, indirect effects, intraguild predation, multiple predator effects, trophic interaction strength.

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INTRODUCTION

Climate change impacts on plants and animals are already evident as shifts in the geographic distribution of species and altered species phenology and life-history (Parmesan 2006; Suttle *et al.* 2007; Post *et al.* 2008). These alterations stand to change the direct effects among species and thereby transform the nature and strengths of indirect effects (Harrington *et al.* 1999; Petchey *et al.* 1999; Schmitz *et al.* 2003; Voigt *et al.* 2003; Winder & Schindler 2004; Wilmers & Post 2006; Memmott *et al.* 2007; Suttle *et al.* 2007; Both *et al.* 2008; Tylianakis *et al.* 2008; Barton *et al.* 2009). But, predicting exactly what these changes will be is limited by uncertainty about how mechanisms of direct and indirect species interactions will change (Schmitz *et al.* 2003; Tylianakis *et al.* 2008).

Current mathematical theory predicting warming effects on food chains (e.g., Emmerson *et al.* 2004, 2005; Vasseur & McCann 2005) provides an important step to encourage research to reduce this uncertainty. Such theory assumes that there are single species within each trophic level of a food chain (or implicitly that all species within a trophic level are functionally identical) and it focuses on interaction

strength as the principle driver of food chain dynamics. Yet, multiple species within trophic levels may not be functionally identical for at least two reasons. First, species are unlikely to have identical interaction strengths (Hall & Raffaelli 1993; Wootton & Emmerson 2005). Second, species' traits can determine the mechanisms of direct and indirect interactions (Duffy 2002; Schmitz 2007; Violle *et al.* 2007). For example, predator-hunting mode (e.g. active pursuit, sit-&-wait ambush) is an important functional trait that determines whether or not indirect effects of predators are largely mediated by consumptive or non-consumptive effects of predators on prey (Schmitz 2008). Indeed, the nature of climate effects on predator-prey interactions may depend on predator hunting mode (Wilmers *et al.* 2007).

Because these biological details are not captured by mathematical theory, we instead motivate our research using theory derived from empirical synthesis of multiple predator effects (Schmitz 2007). This theory predicts that the nature of multiple predator effects on communities depends on two species attributes, predator hunting mode and predator and prey habitat domain, where habitat domain defines a species' microhabitat choice and spatial extent of movement within the chosen microhabitat. In as much as climate

change can alter microhabitat choice and movement of species, then climate effects on species' habitat domain should explain variation in the nature and strength of trophic interactions.

We report on an experiment in a New England, USA grassland that evaluates this assertion by examining how warming consistent with expectations for this region influences the nature of cascading multiple predator effects. Previous research in this system revealed that two focal

predator species (an active hunting jumping spider *Phidippus rimator*, and a sit-&-wait ambush spider *Pisaurina mira*), are spatially segregated in the vegetation canopy (Fig. 1). Individually they cause either consumptive or non-consumptive effects on a common grasshopper herbivore prey species *Melanoplus femurrubrum* (Schmitz & Suttle 2001). *P. rimator* exerts a positive indirect effect on all plants, as this active hunting predator reduces prey density without altering their diet composition. *P. mira* has no net density effect on grasshoppers (i.e., predation mortality is compensatory to natural grasshopper mortality). However, it causes a grasshopper diet shift that results in increased grasshopper impact on herbs and a decreased impact on grasses (Schmitz & Suttle 2001). Collectively, the predators have linear (averaging) effects on their shared herbivore prey (Sokol-Hessner & Schmitz 2002), their prey's grass and herb resources (Schmitz & Sokol-Hessner 2002) and on ecosystem functions (Schmitz 2009).

We show how experimental warming transforms this system by altering the predator species' habitat domain, and hence the nature of multiple predator direct effects on prey and indirect effects on plants.

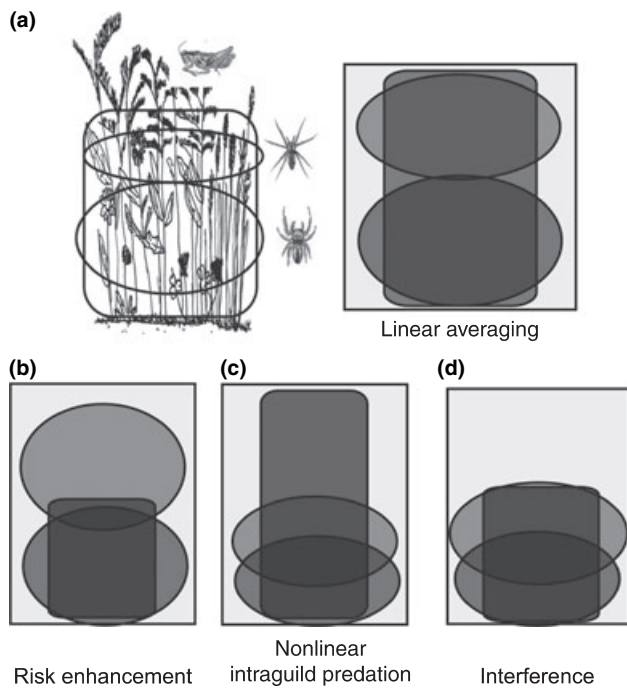


Figure 1 Contingent multiple predator effects on a common prey species using the concept of predator and prey habitat domain. The drawing in the upper left depicts the vertical and horizontal location within a grassland habitat of grasshoppers (rounded rectangle) and spiders (ellipses). The figure depicts that the grasshopper habitat domain is the entire vegetation canopy whereas the sit-&-wait spider resides in the upper canopy and the active hunting spider resides in the middle canopy. This concept can be translated to predict conditions leading to different multiple predator effects on shared prey. (a) Predators are expected to have linear average effects whenever predators have spatially complementary habitat domains and prey habitat domains overlap completely with that of all predators. (b) Predators are expected to have risk enhancing effects whenever predators have overlapping habitat domains but the prey only occupies space used by only one predator species. (c) Predators are expected to have risk reducing effects due to intraguild predation whenever predators have overlapping habitat domains and prey have habitat domains broad enough to have a refuge from all predators. (d) Predators are expected to have risk reducing effects due to interference interactions when they and their prey have completely overlapping habitat domains.

BACKGROUND THEORY AND PREDICTIONS

Predator functional trait effect

Predators can propagate indirect effects by altering the numerical abundance of herbivore prey by capturing and consuming them, or causing prey to modify foraging activity and habitat use in a manner that reduces predation risk (Schmitz 2008). Empirical synthesis indicates that these different kinds of effect are related to predator hunting mode, irrespective of taxonomic identity (Schmitz 2007). Sit-&-wait ambush predators cause largely behavioural responses in their prey; widely roaming, actively hunting predators may reduce prey density. These different direct effects, should lead to hunting mode-dependent differences in indirect effects on plant resources (Schmitz 2004).

Multiple predator effects

Empirical synthesis (Schmitz 2007) has revealed that generally, there are four kinds of emergent multiple predator effects and they are contingent on the way habitat domain of predators and prey overlap (Fig. 1).

The effect of multiple predators on a shared prey should be the linear average of individual predator effects whenever predators have spatially complementary habitat domains and prey species have broad habitat domains (Fig. 1a). This arises because there is little if any opportunity for predators to engage in interspecific interactions. The prey then encounters the average level of predation risk throughout

its habitat domain. In turn, the strength of multiple predator effects on the resources of the prey (i.e., strength of indirect effect) should be the average of the individual predator species effects.

Empirical synthesis (Schmitz 2007) shows that nonlinear risk enhancement may occur whenever prey species have narrow habitat domains and predator species have broad but overlapping habitat domains (Fig. 1b). This appears to arise because prey have limited recourse to escape their predators because their habitat domain is nested within that of their predators. Also, predator species can roam more broadly than their prey, and thus subsidize their needs elsewhere reducing the potential for intraspecific interactions arising from limiting abundance of shared prey. In this case, predator indirect effects on the prey species' resources should be enhanced relative to single predator treatments (Schmitz 2007).

Nonlinear risk reduction arises from either intraguild predation or interference interactions. Empirical synthesis (Schmitz 2007) revealed that intraguild predation may arise whenever prey species have broad habitat domains and predators have overlapping narrow habitat domains (Fig. 1c). In this case, prey can evade predators by seeking out spatial locations that neither predator accesses. With no other prey, predators hunt each other. Interference interactions arise when both prey and predator have either broad or narrow habitat domains but overlap completely in space (Fig. 1d). Empirical synthesis (Schmitz 2007) shows that these conditions lead to interspecific aggression as predators vie for and defend hunting locations in space. In both cases, the strength of the indirect effect should weaken in proportion to the degree to which individual predator species effects are weakened in a multiple predator setting.

Potential effects of warming

Habitat selection by spiders and grasshoppers involves a trade-off between maximizing resource intake, minimizing the likelihood of engaging in negative interspecific interactions, and maintaining thermal homeostasis (Schmalhofer 1999; Pitt 2000; Joern *et al.* 2006; Wolensky & Logan 2007). This trade-off arises because total daily activity is thermally constrained (Uvarov 1977; Belovsky & Slade 1986; Schmalhofer 1999). But, species will differ in their weighting of the trade-off components. Grasshoppers have greater thermal tolerances than spiders and are thus less likely to be thermally stressed (Li & Jackson 1996; Joern *et al.* 2006). Spider taxa differ in their thermal tolerances and temperature preferences in their habitats (Schmalhofer 1999).

Within the vegetation canopy of the grassland there is a vertical temperature profile in which maximum temperature is highest near the top of the canopy and decreases downward toward the ground surface (Fig. S1). Environ-

mental warming maintains this temperature profile but absolute temperatures at each elevation is higher than in ambient conditions (Fig. S1).

Accordingly, to remain within the range of their thermal tolerances we may expect that the grasshopper and the two spider species will adjust their habitat domains downward in the canopy in response to warming. The degree of adjustment made by each species will determine the nature of the emergent nonlinear multiple predator effect. If herbivores adjust their habitat domain, but predators do not, then we should see nonlinear risk enhancement where prey should experience higher predation mortality than in ambient conditions (Fig. 1b). This should intensify the strength of the indirect effect of predators on plants. If herbivores do not change their habitat domain but predators do, then we should see nonlinear risk reduction through intraguild predation (Fig. 1c). In this case, one species of predator (the intraguild prey) should experience higher mortality and prey should experience lower mortality than in ambient conditions leading to a weakening of top-down indirect effects. Finally, if herbivores and predators increasingly overlap in habitat domain, we should see nonlinear risk reduction through interference (Fig. 1d). In this case, we should see prey experience lower mortality than in ambient conditions and a weakening of predator indirect effects on plants.

METHODS

We tested the above theory by evaluating interactions at three organizational levels in control (ambient temperature) and warmed conditions: (1) behavioural level (measuring predator and prey movement and habitat domain); (2) population level (measuring predator and prey mortality); (3) food web level (determining the nature of and measuring the strength of indirect effects on grasses and herbs). We conducted our experiment in a grassland ecosystem in northeastern Connecticut, USA, comprised of grasses and herbs, the generalist grasshopper *M. femurrubrum*, and the sit-&-wait predator *P. mira* and active hunting predator *P. rimator*.

Behavioural level

During July and August 2008 we observed 3rd instar *M. femurrubrum*, adult *P. mira*, and *P. rimator* in terraria. We constructed terraria from a 45 × 30 cm rectangular plywood base that contained sod cut from the same fields in which we conducted the population and food chain experiments. The sod and vegetation were enclosed by a 75 cm tall piece of aluminum insect screen that was securely attached to the wooden base at the bottom and a 45 × 30 cm insect screen lid at the top to prevent arthropods from escaping during

the experiments. We drew a grid of 15×15 cm quadrats on each side of each terrarium to quantify movement in three-dimensional space. The terraria were placed on bench tops outdoors in a grass field and exposed to ambient light, temperature, and moisture.

We stocked into the terraria four *M. femururbrum* grasshoppers with one *P. mira* and one *P. rimator*. The terraria were either left as a control (ambient temperature) or warmed to an average of 3°C above ambient (Fig. S1), which is the predicted temperature increase for this region by 2100 (NERA 2003). Terraria were warmed above the ambient temperature with a single infrared heat lamp (250w, Exo-Terra Heat Wave Lamp, Mansfield, MA, USA) mounted level with the top of each terrarium and ≈ 15 cm from the side. By angling the lamp at 45° toward the terraria, we warmed terraria 3°C above the control and maintained the heat gradient observed in the field (see Fig. S1 for a description of how heat gradients were measured). We randomized the position on the bench tops and treatment of each terrarium between days.

Individual grasshoppers and spiders were collected from local fields with sweep nets, marked with different colours of enamel paint (Testors, Rockford, IL, USA) on their thorax (grasshoppers) or abdomen (spiders). We stocked four grasshoppers, one *P. mira*, and one *P. rimator* into each terrarium 1 day prior to observations. Individuals were observed between 06:00 and 21:00 and their location within the grid was recorded every 30 min. Individuals were removed and released after each observation period. We conducted five observations, using a new complement of individuals during each period to maintain independence among each set of daily observations.

We estimated treatment effects on each species' habitat domain with a log-linear model. For each day we counted the total number of times an individual was observed in each quadrat. We calculated the 5-day average occupancy for each quadrat and tested for treatment effects using JMP v.7 (SAS Institute Inc., Cary, NC, USA). We used a log-linear model to determine if temperature altered grasshopper location in three dimensions during the behavioural observations. We used a log-linear model to test for effects of warming and species identity on spider species three-dimensional location within the observational enclosures. Finally we conducted F-ratio tests using variance of vertical and of horizontal distances of each spider species in control relative to warmed conditions to determine if the spatial extent of vertical and horizontal movement changed with warming.

Population and food web level

During summer 2008 we conducted a standard field enclosure experiment (Schmitz 2004) to assess the effects

of temperature and multiple predators on plant, grasshopper, and spider abundance. We constructed $1.0 \text{ m}^2 \times 0.8$ m cylindrical enclosures using aluminum insect screen secured to vinyl coated garden fencing for sides and fibreglass insect screen to enclose the top. For the warmed treatments, we passively raised the temperature within the enclosure by securing plastic sheeting (4 mm Film-Gard, Covalence Plastics, Minneapolis, MN, USA) to the outer structure of each cage, while leaving the top covered only by screen. This design did not inhibit rainwater from entering cages relative to unwrapped cages ($t_{1,4} = -0.73$, $P = 0.45$). The resulting 'greenhouse effect' warmed the cages $\approx 2.5^\circ\text{C}$ above ambient temperatures and maintained the heat profile similar to that found in the natural field conditions (Fig. S1). Temperatures in ambient and warmed conditions were monitored with Hobo data loggers (Onset Corporation, Pocasset, MA, USA, see Fig. S1). Enclosures were placed over naturally growing vegetation. We selected sites to ensure initially equivalent composition of grasses and herbs (Fig. S2). Enclosures were spaced ≈ 2 m apart to maintain independence. The experimental conditions calibrated well to those expected for naturally warmed conditions at the field site (Barton *et al.* 2009).

The enclosures either were left as a plant-only control (1-level), stocked with grasshoppers (2-level) or with grasshoppers and spiders (3-level) in mid June 2008. We stocked 10 2nd instar grasshoppers and two adult spiders to each enclosure to match field densities at the time of stocking. We stocked the predator species using a replacement series design—which holds total predator density constant but varies predator relative abundance—for two reasons. First, a replacement series approximates natural conditions in the field in which total predator density among 2 m^2 sampling plots varied little whereas the relative abundance of the predator species varied much more (Schmitz 2009). Second, a test of the theory (Schmitz 2007) requires a replacement series design to detect the hypothesized linear and nonlinear effects. This is because in a replacement series design the combined species effects should be the average of the corresponding individual species effects, if predator effects are linear. Deviations from this average indicate nonlinear effects (Sih *et al.* 1998; Schmitz 2007). The treatments were arrayed in a randomized-block experimental design with each treatment represented once in each of five blocks.

The enclosures were surveyed one day after stocking to identify possible stocking-related mortality. When it occurred grasshoppers or spiders were added to the enclosures to restore the initial stocking density. Thereafter, grasshopper and spider numbers were monitored every two weeks until the experiment was terminated after 75 days when all grasshoppers had developed into mature adults. Thus experiment duration covered the majority of the herbivore life cycle. We removed and counted all living

grasshoppers and spiders before clipping all aboveground biomass from within each cage and sorting it into two functional groups: grasses and forbs. Plants were dried at 60 °C for 48 h and weighed.

We examined the effects trophic combinations and warming on final grasshopper abundance and on grass and forb abundance using a randomized block ANOVA followed by a Tukey test whenever a significant difference was detected. We calculated the expected multiple predator effect on grasshoppers and plants for control and warmed conditions respectively by averaging the individual predator species effects. We compared the expected values against their corresponding observed multiple predator effect using one-tailed, one-sample *t*-tests. We calculated the indirect effect magnitude of spiders singly and in combination on grass and herb abundance using the log ratio $[\ln(V_{p+}/V_{p-})]$ where V_{p+} and V_{p-} are respectively grass or herb biomass in the presence (3 level treatment +) and absence (2 level treatment -) of predators (Schmitz *et al.* 2000).

RESULTS

Behavioural level

Figure 2 presents the habitat domains of grasshoppers and spiders under control and warmed conditions. Grasshoppers did not change their location in three dimensional space in response to warming (G^2 tests, $P > 0.15$). Log-

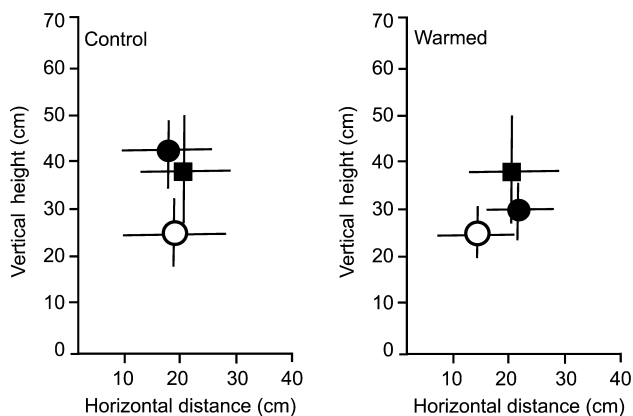


Figure 2 Measured vertical and horizontal locations of grasshoppers (squares) and spiders (solid circles: sit-&-wait; open circles: active hunting) in the vegetation canopy of experimental arenas used to quantify the effects of experimental warming on species' habitat domain. The values depict mean (symbols) and 1 SD in vertical height and horizontal distance from fixed reference points at the side and bottom of the experimental arena. The figure shows that the predators segregate in space and overlap with grasshoppers in ambient control conditions. Experimental warming causes only the sit-&-wait predator to change its location and overlap more with the jumping spider.

linear analysis examining differences in spider species locations in three dimensions under ambient and warmed conditions revealed that there was no significant treatment effect on the mean horizontal location of spiders under control or warmed conditions ($G^2 < 5.099$, $P > 0.08$). However, log-linear analysis revealed a significant treatment effect on the mean vertical height. We found that under ambient conditions, *P. mira* and *P. rimator* were segregated vertically ($G^2 = 24.32$, $P < 0.001$). Experimental warming caused *P. mira*, to move lower down in the canopy ($G^2 = 10.62$, $P < 0.031$), whereas *P. rimator* did not change its vertical location ($G^2 = 1.91$, $P = 0.74$). Consequently, there was no difference in vertical height between spider species under warmed conditions ($G^2 = 4.25$, $P = 0.37$). F-ratio tests revealed that warming did not change the magnitude of the variance in vertical and horizontal locations of grasshoppers or spiders (all $P > 0.10$). Thus, warming caused spiders to increase their overlap via downward shift in *P. mira* habitat domain rather than via increasing the extent (magnitude of variance) of their habitat domains.

Warming did not cause a change in grasshopper habitat domain but it caused the habitat domains of the two spiders to overlap (Fig. 2). This outcome demonstrates a switch from conditions that should lead to linear (averaging) multiple predator effects (Fig. 1a) to the overlapping conditions that should produce nonlinear intraguild predation (Fig. 1c). We next show that we indeed see a switch from linear averaging to nonlinear intraguild predation effects.

Population level

Both active and sit-&-wait spiders in all treatments were recovered at the end of the experiment, with one exception. In the warmed, multiple predator treatment we recovered only the sit-&-wait spider in all five replicates. This outcome is indicative of intraguild predation. It is less indicative of interference competition because high spider species mortality is not expected in multiple predator setting involving interference interactions (Schmitz 2007).

Randomized block ANOVA revealed that predator and warming treatments significantly (Both $F_{4,12} \geq 6.5$, both P 's < 0.01) altered grasshopper abundances relative to control conditions (Fig. 3). The Tukey test revealed that in ambient control conditions, the active hunting spider significantly reduced grasshopper abundance, whereas the sit-&-wait spider did not. Grasshopper abundance in the control multiple predator treatment was statistically intermediate to the two single predator treatments (Fig. 3). Moreover, the multiple predator effect was statistically not different from expectations based on the average of the single predator effects (*t*-test, $P > 0.25$). The Tukey test

revealed that in warmed conditions the active hunting spider significantly reduced grasshopper abundance, whereas the sit-&-wait spider did not have a significant effect. Now, however, grasshopper abundance in the multiple predator treatment was not statistically different from grasshopper abundance in the sit-&-wait predator treatment (Fig. 3). Also, the observed multiple predator effect was statistically different from the expected effect based on the average of the individual predator species effects ($t_4 = 2.24, P < 0.05$) and was biased toward the sit-&-wait predator effect. This outcome is consistent with expectations based on observed mortality of active hunting spiders in the warmed, multiple predator treatment further supporting the interpretation that intraguild effects predominate in warmed conditions.

Food web level

Randomized block ANOVA revealed that trophic manipulations significantly (Both $F_{4,16} \geq 7.25$, both P 's < 0.01) altered grass and herb abundance in both control (unwarmed) and warmed treatments (Fig. 4).

In control conditions, the Tukey test revealed that grasshoppers caused a significant reduction in grass and herb abundance (Fig. 4). Relative to the 2-level grasshopper-only treatment, there was a non-significant increase in grass and herb biomass in the 3-level active hunting spider treatments (Fig. 4). This is indicative of weak positive

indirect effects on grass and herbs (Fig. 5). Alternatively, there was a significant increase in grass biomass and a significant decline in herb biomass in the 3-level sit-&-wait spider relative to the 2-level grasshopper treatment (Fig. 4), indicative of strong positive and negative indirect effects on grass and herbs (Fig. 5). Grass and herb biomass in the 3-level multiple predator treatment was statistically intermediate to the single predator treatments. Moreover, the multiple predator effects did not differ significantly (t -tests, $P > 0.25$) from expectations based on the average of the single predator effects (Fig. 4), resulting in indirect effect magnitudes on grass and herb that were intermediate to the single predator effect magnitudes (Fig. 5).

In warmed conditions, the Tukey test revealed that grasshoppers caused a significant reduction in grass and herb abundance (Fig. 4). Relative to the 2-level grasshopper-only treatment, there was a non-significant increase in grass and herb biomass in the 3-level active hunting spider treatments (Fig. 4), again indicative of weak positive indirect effects on grass and herbs (Fig. 5). There was a significant increase in grass biomass and a significant

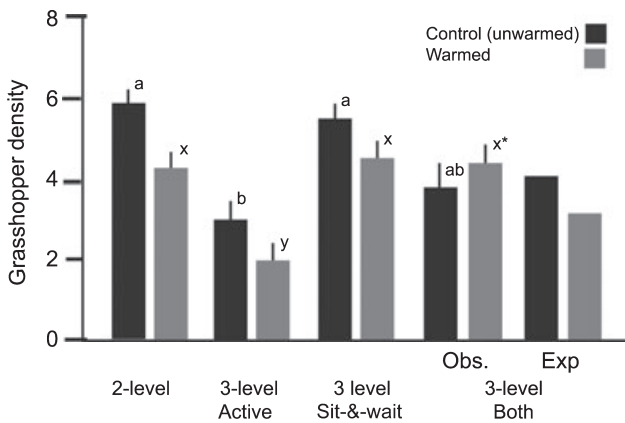


Figure 3 Effects of trophic level manipulations and experimental warming on end-of-season grasshopper abundances in enclosure cages. Treatments are: 2-level grasshopper and plants; and 3-level spider species, grasshopper and plants. Values are mean \pm 1 SE. Letters above the bars identify significantly different treatment means within control and warmed conditions respectively, based on ANOVA followed by a Tukey test. A *signifies a significant difference between the expected multiple predator effect and corresponding observed multiple predator effect based on a one sample t -test.

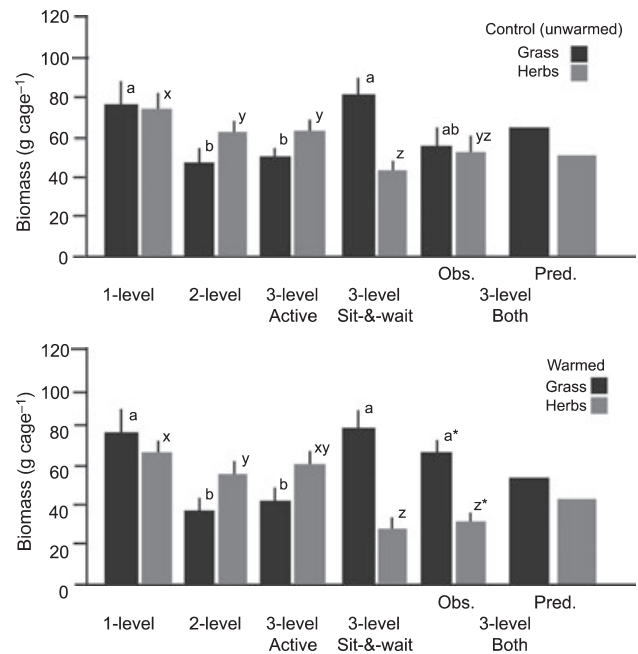


Figure 4 Effects of trophic level manipulations and experimental warming on end-of-season plant abundances in enclosure cages. Treatments are: 1-level plants only; 2-level grasshopper and plants; and 3-level spider species, grasshopper and plants. Values are mean \pm 1 SE. Letters above the bars identify significantly different treatment means within control and warmed conditions respectively, based on ANOVA followed by a Tukey test. A *signifies a significant difference between the expected multiple predator effect and corresponding observed multiple predator effect based on a one sample t -test.

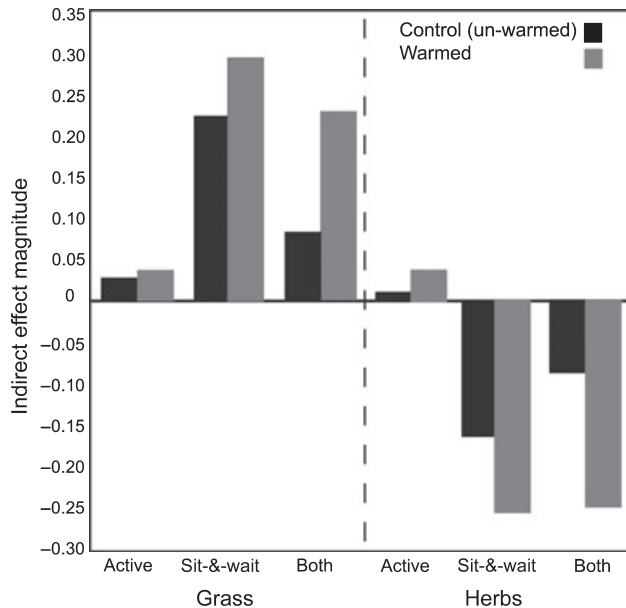


Figure 5 Mean strength of indirect effect of single and multiple spider predators on grass and herbs in control and warmed conditions in the experimental food chains. Values were calculated using plant biomass data presented in Fig. 4.

decline in herb biomass in the 3-level sit-&-wait spider relative to the 2-level grasshopper treatment (Fig. 4), indicative of strong positive and negative indirect effects on grass and herbs (Fig. 5). Unlike control conditions, grass and herb biomass in the 3-level multiple predator treatment was statistically similar to biomass in the sit-&-wait predator treatments (Fig. 4). Moreover, these multiple predator effects differed significantly (t_4 's ≥ 2.2 , $P < 0.05$) from expectations based on the average of the single predator effects (Fig. 4). Accordingly, the indirect effect magnitudes on grass and herb mirrored the strengths observed in the sit-&-wait treatment (Fig. 5).

DISCUSSION

This study shows that the direct and indirect effect of individual spider species on the food chain in both control and warmed conditions depended on hunting mode in ways that were consistent with expectations. Namely, the active hunting jumping spider caused a significant reduction in grasshopper abundance relative to the 2-level predation control (Fig. 3) and it had positive indirect effects on both grasses and herbs (Figs 4 and 5). The sit-&-wait spider had no significant effect on grasshopper density (Fig. 3) but it had a positive indirect effect on grasses and a negative indirect effect on herbs. Experimental warming enhanced the strength of those indirect effects relative to ambient control conditions (Fig. 5).

The study revealed that experimental warming of a magnitude consistent with predicted climate change effects for the study region could, however, alter food chain structure and thus transform its functioning. This transformation came about via altered interspecific interactions that caused a linear multiple predator effect to become nonlinear.

Under ambient control conditions, the combined effect of both predators on their shared grasshopper prey and the prey's grass and herb resources was the linear average of the single predator effects (Figs 3 and 4). This outcome is consistent with theoretical expectations for multiple predator effects when predators have complementary habitat domains and prey overlap completely with all predators (Fig. 1a). Experimental warming, in turn, led to a nonlinear intraguild interaction whose effects cascaded to influence plant community structure (Figs 3 and 4). Consistent with theoretical predictions (Fig. 1c), the intraguild interaction arose because warming caused the predator species' habitat domains to overlap within the vegetation canopy, whereas the habitat domain of the prey remained unchanged. In particular, only the sit-&-wait spider shifted its habitat domain (Fig. 2) by moving lower down into the cooler parts of the canopy (Fig. S1). However, the lack of habitat domain shift came at a cost to the jumping spider as its functional role switched from being an independent predator to an intraguild prey. Consequently, the intraguild interaction was short-lived and resulted in complete loss of the intraguild prey—the jumping spider—from the multiple predator treatments. That this is an intraguild predation effect, rather than a thermal stress effect, is supported further by the observation that all jumping spider individuals were recovered in both control and warmed single predator treatments.

The net effect of the behavioural interaction between predator species was a transformation in food web structure and consequent function in which the multiple predator food web was transformed into a linear chain comprised of the sit-&-wait predator, grasshopper herbivores and grasses and herbs. Accordingly, the magnitude of effect in the warmed multiple predator treatment mirrored that of the warmed sit-&-wait predator treatment (Fig. 5). One concern is that this strong outcome is a potential artefact due to cage size that constrained us to stock only a single individual of two predator species in the multiple predator treatments. We feel, however, that this outcome gives a reasonable approximation of field conditions for several reasons. First, interactions strengths vary little with enclosure sizes ranging from $0.25 \text{ m}^2 \times 0.8 \text{ m}$ to $1 \text{ m}^2 \times 0.8 \text{ m}$, and between enclosures and 2 m^2 open field plots (Schmitz 2004; Barton *et al.* 2009). Second, while both spider species naturally coexist, the jumping spider can be quite rare in locations where the sit-&-wait spider is highly abundant (Schmitz

2009). Furthermore, when the sit-&-wait spider dominates, the net top-down effects on the community converge on the net effects when this predator species exists alone (Schmitz 2009).

Top-down predator effects interact with warming to influence grasshopper abundances in this experiment. Warming caused grasshopper survival to decline relative to control conditions, across 2-trophic level and 3-trophic level single predator treatments. But, the magnitude of decline varied by treatment ranging from 7% to 37% (Fig. 3). Alternatively, the multiple predator, warmed treatment increased grasshopper survival by 20% relative to the control due to the loss of averaging effect and convergence on the magnitude of the single sit-&-wait predator effect (Fig. 3).

Bottom-up, productivity effects could also mediate top-down effects, but this likelihood is low. Net primary productivity was effectively quantified using the 1-level plant-only treatments (Fig. 4). This treatment revealed no significant difference (pooled *t*-tests, $P > 0.08$) in grass and herb biomass between control and warmed conditions (Fig. 4). The finding that experimental warming did not affect primary production (Fig. 4) is consistent with insights from a synthesis of climate effects on this grassland system (Barton *et al.* 2009) that reported no relationship between interannual growing season temperature and primary production over the same range of temperatures. Thus, the lack of a bottom-up productivity effect of warming is unlikely to be an artefact of the experiment. An alternative bottom-up effect of warming on trophic interactions may be that it alters plant phenology (Post *et al.* 2008). While not quantified in this study, warming may alter the relative abundance of grasses and forbs at different times during the growing season, thereby changing the trade-off between grasshopper resource selection and predator avoidance. The degree to which this may explain variation in the strength of top-down control and, indeed the degree to which it alters predator-predator interactions requires further detailed evaluation.

This study contributes toward general understanding of multiple predator effects in two respects. First, it is motivated by general theory (Schmitz 2007) that predicts how multiple predator effects on shared prey should vary with the spatial juxtaposition of their habitat domains. We provide an explicit test of this theory using warming as a perturbation intended to change habitat usage by the predators and prey. Consistent with theory, we observed a switch from linear to nonlinear intraguild effects. Second, the empirical insight, that intraguild predation lead to the loss of the intraguild prey and thereby strengthened top-down effects, supports predictions of theory on the role of intraguild predation in trophic cascades (Diehl & Feissel 2000; Krivan & Diehl 2005).

There is concern that climate change stands to alter the nature and strength of species interactions in ecological communities (Schmitz *et al.* 2003; Voigt *et al.* 2003; Winder & Schindler 2004; Wilmers & Post 2006; Both *et al.* 2008; Tylianakis *et al.* 2008). This concern is especially relevant for systems in which top predators may play important roles in regulating the dynamics of prey species and indirectly affecting the resources of their prey species. Loss of predator diversity may fundamentally alter system functioning (Schmitz *et al.* 2003; Wilmers & Getz 2005; Wilmers & Post 2006; Wilmers *et al.* 2007; Tylianakis *et al.* 2008). Accumulating evidence suggests that multiple predator interactions can buffer the effects of climate warming and thereby preserve predator species and functional diversity (Wilmers & Getz 2005; Wilmers & Post 2006). Our study contributes to understanding of climate change on predator effects by suggesting that predator functional diversity may also become diminished as a consequence of climate-altered predator-predator interactions. This loss of predator diversity can have important repercussions for the nature and strength of trophic effects on ecosystem function (Schmitz 2008, 2009).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Heat profiles for field (open) and behavioural (closed) experiments.

Figure S2 Plant community composition at the initiation of the 2008 field experiment.

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