Predicted climate change alters the indirect effect of predators on an ecosystem process

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Changes in rainfall predicted to occur with global climate change will likely alter rates of leaf-litter decomposition through direct effects on primary decomposers. In a field experiment replicated at two sites, we show that altered rainfall may also change how cascading trophic interactions initiated by arthropod predators in the leaf litter indirectly influence litter decomposition. On the drier site there was no interaction between rainfall and the indirect effect of predators on decomposition. In contrast, on the moister site spiders accelerated the disappearance rate of deciduous leaf litter under low rainfall, but had no, or possibly a negative, indirect effect under high rainfall. Thus, changes resulting from the more intense hydrological cycle expected to occur with climate change will likely influence how predators indirectly affect an essential ecosystem process.

detrital food web | litter decomposition | rainfall | spiders | trophic cascade

Climate-change models predict a more intense hydrological cycle with both increases in rainfall and increased length and severity of droughts (1, 2). Changes in rainfall will likely affect ecosystem processes such as primary production and nutrient release from decomposing litter caused by direct effects of altered rainfall on plants and primary decomposers, respectively. For example, low moisture can inhibit fungal growth and/or activity (3, 4). Changes in rainfall may also alter how trophic interactions indirectly influence rates of ecosystem processes. Recent research has shown that climatic changes may have large impacts on how predators indirectly alter net primary production through trophic cascades (reviewed in refs. 5–8). In detritus-based food webs predators have the potential to influence indirectly the amount of leaf litter through trophic interactions that affect rates of decomposition. This chain of interactions is a trophic cascade (9–12) analogous to the classic cascade affecting living plants. In grassland systems litter in cages accessible to large arthropod predators exhibited lower rates of litter disappearance compared with predator-exclusion cages (13, 14), although other similar experiments in grasslands revealed a negligible impact of these predators on decomposition rate (15). In a forest-floor system, experimentally reducing spider numbers also accelerated the rate of disappearance of a straw test litter (16). However, a longer-term experiment using natural canopy litter produced an opposite effect, with litter decomposing more rapidly at higher spider densities (12). This extreme variation in the sign of the indirect effect of spiders and other predators on decomposition, from negative through zero to positive, may at least partly reflect differences in abiotic factors between sites and years. The unexpected enhancement of decomposition by spiders in the forest-floor experiment occurred during a period of unusually low rainfall (12), which suggests that large changes in moisture, such as those predicted by climate-change models, may affect the sign of spider-induced cascades in the detrital web. Because litter quality also varied between the experiments conducted on the forest floor, a direct test of this hypothesis is needed.

We designed a field experiment to test the hypothesis that altered rainfall of the magnitude predicted by climate-change models affects the sign of the spider-induced trophic cascade in the food web of deciduous leaf litter. The complexity of interactions and indirect effects in such complex systems makes it difficult to predict the impact of changes in abiotic factors on ecosystem processes by experimenting with simplified components that may be unrepresentative of the dynamics of the entire system (8). Therefore, we used replicated, isolated sections of the intact forest-floor food web. We manipulated spider numbers in replicated 0.5-m^2 plots (natural spider density or low spider density) that were located inside 14-m^2 plots in which rainfall was manipulated (high-rainfall, low-rainfall, and ambient-rainfall treatments). Because the forest floor is highly heterogeneous, we replicated the rainfall treatments twice in each of two sites ≈0.5 km apart. Three bags with canopy leaf litter were placed in each 0.5-m^2 plot and periodically collected. We predicted that under high-rainfall conditions spiders would have a negative or no impact on the rate of litter disappearance, whereas we expected low rainfall to alter the sign of the trophic cascade, causing spiders to indirectly enhance litter decomposition.

Results

Spider Manipulation. The activity–density of wandering spiders (species that do not construct webs) was two times higher in the natural spider density compared with low-density treatments (Fig. 1; $t_{11} = 3.02$; $P = 0.01$), and their absolute density was 1.3 times higher in the natural spider density treatment (Fig. 1; $t_{11} = 2.37$; $P = 0.04$). There were no significant differences between spider density treatments for web-spinning species (Fig. 1; $P > 0.2$). The extent to which the spider removal/exclusion procedures altered densities of wandering or web-spinning spiders did not differ between sites or rainfall treatments ($P > 0.2$).

Trophic Cascades. We found a significant interaction between rainfall treatment and site ($F_{2,6} = 6.31, P = 0.03$). In site 1 rainfall did not alter the trophic cascade (Fig. 2*a*; $F_{2,3} = 0.46, P = 0.67$), and the index was close to zero (i.e., spiders had little impact on litter disappearance regardless of rainfall treatment at this site). In contrast, rainfall affected the sign and magnitude of the trophic cascade in site 2 (Fig. 2*b*; $F_{2,3} = 26.18, P = 0.013$). The trophic cascade under low-rainfall conditions differed from that under both high-rainfall conditions [$P = 0.008$, Fisher's least significant difference (LSD); $P = 0.017$, Tukey's honestly significant difference (HSD)] and ambient conditions ($P = 0.008$, Fisher's LSD; $P = 0.016$, Tukey's HSD). The trophic cascade was similar in high-rainfall and ambient plots ($P = 0.90$). Under low-rainfall conditions decomposition was ≈20% faster at natural spider densities compared with the low spider density treatment; in contrast, under both high-rainfall and ambient conditions, spiders did not affect, or possibly even hindered, rates of litter disappearance (Fig. 2*b*).

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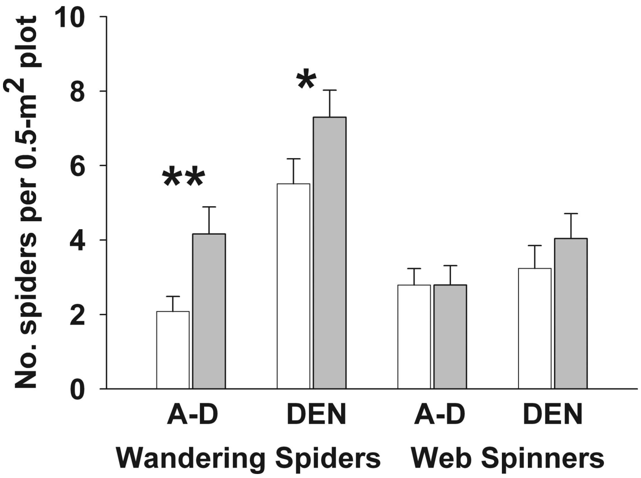

Fig. 1. Activity–density (A-D; number caught in pitfall traps) and absolute density (DEN; number found searching the litter) of wandering spiders and web-spinning spiders in the low spider (open bars) and natural spider (filled bars) density treatments pooled over rainfall treatment and site. Values graphed are means ± SE. *, $P \leq 0.05$; **, $P \leq 0.01$.

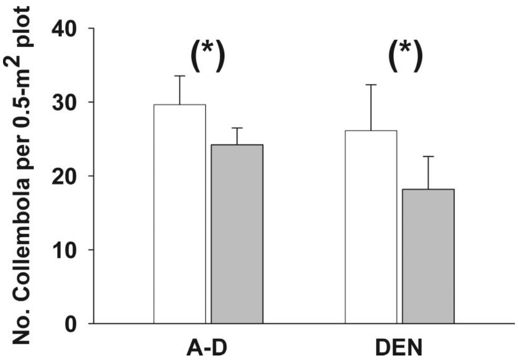

Fig. 3. Activity–density (A-D) and absolute density (DEN) of large, surface-active Collembola (Entomobryidae and Tomoceridae combined) in the low spider (open bars) and natural spider (filled bars) density treatments pooled over rainfall treatment and site. (*), $P \leq 0.08$. Values graphed are means ± SE.

Collembola. In the forest-floor food web, Collembola affect litter disappearance directly by feeding on litter and indirectly through litter comminution, inoculation with microbes, and fungal grazing (17). Numbers of the large-bodied, active Collembola (numbers of Entomobryidae and Tomoceridae combined) were marginally higher at lower spider densities compared with the treatment with natural densities of spiders (Fig. 3; $t_{11} = -2.13$, $P = 0.06$, activity–density; $t_{11} = -1.91$, $P = 0.08$, absolute density). The degree to which Collembola numbers responded to the spider-density manipulation did not differ between sites or rainfall treatments ($P > 0.2$).

Soil Moisture. The soil in site 1 was drier than in site 2, based on differences between sites in how the rainfall treatment affected soil moisture ($F_{2,6} = 5.08$, $P = 0.05$, site × rainfall interaction). Soil in the low-rainfall treatment was drier in site 1 than in site 2 (59 ± 11 vs. 28 ± 5 centibars, respectively). Site 2 was in a slight depression, whereas the land sloped slightly away from site 1. Differences in soil moisture readings and topography suggest that site 1 was better drained and that not only the soil but also the leaf litter may have dried out faster in this site.

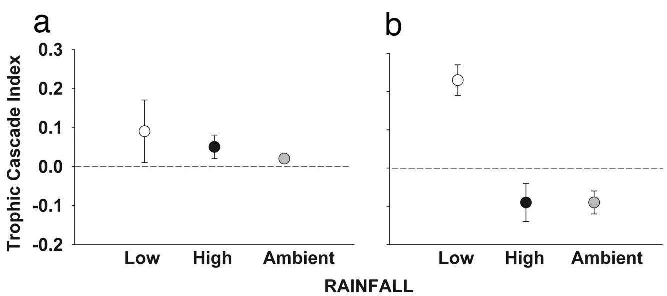

Fig. 2. Effect of rainfall on the strength of the spider-induced trophic cascade expressed as a trophic cascade index. A value of the trophic cascade index near zero reflects the absence of a trophic cascade, a positive value indicates that natural spider densities accelerated litter decomposition, and a negative value indicates that natural spider densities inhibited decomposition. Because of the significant interaction between rainfall treatment and site, results are presented separately for site 1 (*a*) and site 2 (*b*). Values graphed are means ± SE.

Discussion

Results from site 2 support the hypothesis that climate-induced changes in rainfall can alter the sign of the indirect effect of spiders on rates of litter decomposition in deciduous forests. Wandering spiders are clearly implicated as initiators of this trophic cascade. Previously detected cascades in this forest were also associated with substantially altered densities of wandering, but not web-spinning, spiders (12, 16). Web-spinning spiders might also indirectly affect decomposition, but to date it is the wandering spiders whose densities have been most effectively manipulated in field experiments. Because the effectiveness of the spider manipulation in our experiment did not differ between rainfall treatments, changes in rainfall must have altered indirect effects of wandering spiders on lower trophic links.

In this and previous experiments, the indirect effect of wandering spiders on the rate of decomposition, whether positive or negative, is consistently associated with their limitation of densities of active, large-bodied Collembola, the tomocerids and entomobryids. The Tomoceridae, known to be high-quality prey for a major group of wandering spiders, the Lycosidae (18), was the only Collembola family to increase in a long-term removal experiment of wandering spiders in this forest (19). In all trophic-cascade experiments in forest leaf litter, it is primarily the tomocerids or entomobryids that increased in response to reduced densities of wandering spiders (refs. 12 and 16 and this study). Thus, decreased rainfall most likely changes the sign of the spider-initiated trophic cascade by altering the way in which these Collembola interact with fungi, a major resource of Collembola and an abundant primary decomposer in forest leaf litter.

Collembola affect litter disappearance directly by feeding on litter and indirectly through litter comminution, inoculation with microbes, and fungal grazing (17). Intermediate levels of fungal grazing by Collembola can stimulate fungal growth and promote litter decomposition, whereas overgrazing can depress fungal populations, causing a decline in rates of decomposition (20, 21). Thus we hypothesize that wandering spiders consistently depress populations of active, large-bodied Collembola, but the impact of lowered Collembola numbers on decomposition depends on how moisture affects the Collembola–fungus interaction. We propose that during periods of normal to above-average rainfall, Collembola usually enhance litter decomposition by promoting fungal growth; thus, spider depression of Collembola populations will either lower rates of litter decomposition or have minimal impact, depending on Collembola densities and the extent to which spider predation limits Collembola numbers. We hypothesize that extremely dry conditions stress fungal populations enough that they are highly susceptible to overgrazing by Collembola; thus under drought conditions,

ECOLOGY

spiders can enhance decomposition by preventing overgrazing of fungi by Collembola.

The effect of rainfall on the spider-initiated cascade differed between sites. The pattern of this spatial variation is consistent with the proposed mechanism for how changes in rainfall can influence the trophic cascade. Altering rainfall did not affect the cascade index in site 1, which was better drained and drier than site 2. We hypothesize that the fungal community in the litter and soil of site 1 had higher densities of species better adapted to dry conditions, making that community less sensitive to Collembola overgrazing under the low-rainfall treatment.

This proposed mechanistic hypothesis remains to be tested, and even if it is confirmed, the net impact of changes in rainfall on decomposition can still only be predicted by knowing the net result of potentially myriad direct and indirect effects on primary decomposers in different environments. The major contribution of our experiment relates directly to the degree of realism of the experimental units, which were portions of the forest floor that retained the natural complexity of the arthropod-dominated food web of leaf litter. This experiment provides additional evidence that changing rainfall may alter predator-induced indirect effects on lower trophic levels and is an example of how such a change may alter the trophic cascade in a detritus-based web. The indirect effects of wandering spiders on decomposition under low rainfall at site 2 occurred in response to relatively small changes in spider densities, of the magnitude expected to occur naturally over the forest floor and from year to year. Changes in rainfall that altered the sign of the spider-induced trophic cascade reflect natural variation in mean rainfall amounts. An unusually dry year first suggested the hypothesis (12), and during our study, which was conducted in the same forest, the weather was unusually wet. Ambient rainfall was 29% above average, a deviation from normal similar to the high-rainfall treatment. Thus the range of low- and high-rainfall treatments that we used, which was based on the 100-year average, occurred over the course of just a few years. The extremes in rainfall that we imposed fall within the range predicted by models of climate change, although models also predict increased variance in precipitation (1, 2). We altered the mean amount of rainfall and only slightly altered the variance. Extreme temporal variation, particularly prolonged drought, is likely to have impacts on the spider-initiated trophic cascade even greater than we observed.

Understanding how changes in rainfall may affect ecosystem processes such as litter decomposition and the release of nutrients to the forest is critical to predicting systemwide responses to global climate change. Our experiment suggests that one component of this response to climate change will be the manner in which altered rainfall modifies the cascading indirect effects of spiders on rates of litter decomposition.

Materials and Methods

Experimental Design. In March 2001 we established 12 14-m^2 plots (2.5×5.5 m) in a temperate deciduous forest in central Kentucky (oak, maple, hickory, and scattered pine) and randomly assigned them to one of three rainfall treatments: ambient rainfall, low rainfall, and high rainfall. The low- and high-rainfall plots were fenced with aluminum flashing, covered with a 20-m^2 rainout shelter, and subjected to 30% below or 30% above the long-term (100 years) mean rainfall, respectively, whereas the ambient-rainfall plots were unfenced, uncovered, and exposed to ambient rainfall. Rainwater was collected from the rainout shelter roofs by using a gutter system that funneled water into reservoirs. Tarps were also used to collect water for the reservoirs. Low-rainfall plots were irrigated alternating weeks, whereas high-rainfall plots were irrigated weekly. Climate models predict that rainfall in Kentucky will increase in the spring, summer, and fall, but little change is expected in the winter (22). Consistent with these predictions, and because of constraints imposed by freezing temperatures during winter, plots were irrigated from June to December 2002, May to December 2003, and April to December 2004. We established the 12 plots in two sites in the forest ≈0.5 km apart. Six plots were located in each site, with each rainfall treatment replicated twice in each site.

To investigate the effect of rainfall on spider-induced trophic cascades, we constructed 48 0.5-m^2 plots by using 36-cm aluminum flashing buried ≈8 cm in the ground. The low spider density plots ($n = 24$) were completely enclosed with aluminum flashing, and a 10-cm horizontal lip was riveted to the top of the fencing to further impede spider movement. Plots of the natural spider density treatment ($n = 24$) had openings in each wall to allow spiders to move freely into and out of the plot. We installed two of each plot type in each 14-m^2 plot from April 7–18, 2003. For photographs of the 14-m^2 plots, rainout shelters, irrigation system, and 0.5-m^2 plots, see Figs. 4–7, which are published as supporting information on the PNAS web site.

Spider Manipulation and Arthropod Sampling. From April 28 to May 1, 2003 we sifted all of the litter in each 0.5-m^2 plot through a 13-mm mesh screen to locate spiders. Spiders from the natural spider density plots were returned to those plots, whereas spiders found in the low spider density plots were removed and placed in the surrounding litter within the 14-m^2 plot. In the first litter sift, 344 spiders were removed from all plots in the low spider density treatment; a day later the litter was sifted again, and 145 spiders were removed from these plots. Thus an average of ≈20 spiders was initially removed from each low spider density plot. In April and July 2004 we sifted all 0.5-m^2 plots again to continue the low spider density treatment and estimate densities of spiders and Collembola in both spider density treatments. All arthropods were counted and returned, with the exception of spiders found in the low-density plots, which were removed and placed in the surrounding litter within the 14-m^2 plot. We used live pitfall traps to measure activity–densities of arthropods and continually trap and remove spiders from the low spider density plots. Traps were opened for 24-h periods seven times in 2003 from July through September and 19 times in 2004 from May through October.

Rate of Litter Decomposition. White oak (*Quercus alba*) and red maple (*Acer rubrum*) leaves were air dried to a constant weight and broken into ≈5-cm-diameter pieces. Measured amounts (≈2.5 g of oak litter and 2.2 g of maple litter) were placed in separate bags of 6-mm nylon mesh. One maple and two oak litterbags were placed in each 0.5-m^2 plot on May 1, 2003. One oak litterbag was removed from each plot on September 1, 2004, one maple litterbag was removed from each plot on October 13, 2004, and the last oak litterbag was removed on November 29, 2004. Litterbags were dried for 96 h at ≈40°C, and the dried litter was weighed to assess the proportion of litter disappearing.

Soil Moisture. Two Watermark (Irrometer, Riverside, CA) soil moisture sensors (7.6 cm long) were buried in each 14-m^2 rainfall treatment plot to a depth of 13 cm, leaving 5 cm of soil on top of each sensor. Sensors were monitored each week before irrigation. Measurements are in centibars, with a higher reading indicating drier soil.

Statistics: Effect of Rainfall on the Trophic Cascade. Because spider-density treatments were replicated within rainfall treatments, treatment effects on the rate of litter disappearance were not independent. Thus, the interaction between rainfall and spider density in a standard two-way ANOVA could not be used to test for the impact of rainfall on the spider-induced trophic cascade. A repeated-measures ANOVA that adjusts for the nonindependence is one option; however, the relatively low number of replicates makes this approach overly conservative. Furthermore, the third factor in the design, site, is a random factor, and a mixed-model repeated-measures ANOVA is not a straightforward analysis. We used a more direct and conceptually simpler approach that allowed the incorporation of site as a random factor and made it possible to test directly for the effect of rainfall on the strength and sign of the trophic cascade.

We first calculated, for each 14-m^2 rainfall replicate, an index of the strength of the spider-induced trophic cascade. This index reflected the difference in the rates of litter disappearance between spider-density treatments within the 14-m^2 plot. The rate of litter disappearance was calculated by averaging the proportion of litter disappearing from the three litterbags for each 0.5-m^2 replicate of a spider-density treatment and then averaging the proportion disappearing for the two replicates of each spider-density treatment in each 14-m^2 plot. The index of the strength and sign of the trophic cascade was calculated as:

$$\text{trophic cascade index} = \frac{\text{rate at natural spider density} - \text{rate at low spider density}}{\text{rate at low spider density}}, \quad [1]$$

where rate is the rate of litter disappearance. A value of the trophic cascade index near zero reflects the absence of a trophic cascade, a positive value indicates that spiders accelerated litter decomposition, and a negative value indicates that spiders inhibited decomposition. We then used a mixed-model ANOVA to examine impacts of site (random factor) and rainfall treatment (fixed factor) on the trophic cascade index.

Statistics: Spiders. To determine the extent to which the spider-removal procedures reduced spider numbers (activity–density from pitfall trapping and absolute density from sifting the litter), for each 0.5-m^2 plot we calculated a single value for each measure by averaging all pitfall captures for 2003 and 2004, or counts from the two litter sifts in 2004. We then averaged the data from the two replicates in each 14-m^2 plot to obtain a single estimate of activity–density or absolute density for each spider-density treatment within each 14-m^2 plot. We performed paired t tests on these values, pooling rainfall treatments and sites, to give a measure of the simple effect of the removal/exclusion procedure on spider numbers. We elected to use this conservative approach and did not use a more complicated ANOVA for the reasons given above, i.e., the nonindependence of rainfall and spider-density treatments, and the difficulty of incorporating site as a random factor into such a design.

To determine whether rainfall treatment or site affected the extent to which the spider removal/exclusion procedures altered spider numbers, we calculated an index of the difference in spider numbers between treatments analogous to the trophic cascade index and used the same mixed-model ANOVA.

Statistics: Collembola. We analyzed the effect of the spider-density treatment on Collembola numbers in the same way as for spider numbers, using data from both pitfall trapping and litter sifting. We first calculated the simple effect of the spider manipulation on Collembola numbers with a paired t test and then examined the impacts of rainfall and site on the response to the spider manipulation with mixed-model ANOVA by using an index of the difference in Collembola numbers between spider-density treatments.

Statistics: Soil Moisture. Data were averaged for 2003 and 2004, the period when spider densities were manipulated. Average soil moisture per 14-m^2 plot was analyzed by using mixed-model ANOVA with site as a random factor and rainfall treatment as a fixed effect.

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1. Houghton JT (1997) *Global Warming: The Complete Briefing* (Cambridge Univ Press, Cambridge, UK).
2. Intergovernmental Panel on Climate Change (2001) *Climate Change 2001: Impacts, Adaptation, and Vulnerability* (Cambridge Univ Press, Cambridge, UK).
3. Griffen DM (1963) *Biol Rev* 38:141–166.
4. Schnürer J, Clarholm M, Boström S, Rosswall T (1986) *Microb Ecol* 12:217–230.
5. Harrington R, Woiwod I, Sparks T (1999) *Trends Ecol Evol* 14:146–150.
6. Stenseth NC, Mysterud A, Ottersen G, Hurrell JW, Chan K, Lima M (2002) *Science* 297:1292–1296.
7. Walther G, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J, Hoegh-Guldberg O, Bairlein F (2002) *Nature* 416:389–395.
8. Schmitz OJ, Post E, Burns CE, Johnston KM (2003) *Bioscience* 53:1199–1205.
9. Pace ML, Cole JJ, Carpenter SR, Kitchell JF (1999) *Trends Ecol Evol* 14:483–488.
10. Scheu S, Setälä H (2002) in *Multitrophic Level Interactions*, eds Tscharntke T, Hawkins BA (Cambridge Univ Press, Cambridge, UK), pp 223–266.
11. Wardle DA (2002) *Communities and Ecosystems: Linking the Aboveground and Belowground Components* (Princeton Univ Press, Princeton).
12. Lawrence KL, Wise DH (2004) *Pedobiologia* 48:149–157.
13. Kajak A, Chmielewski K, Kaczmarek M, Rembialkowska E (1991) *Pol Ecol Stud* 17:289–310.
14. Kajak A (1997) *Agric Ecosyst Environ* 64:53–63.
15. Kajak A (1995) *Eur J Entomol* 92:573–580.
16. Lawrence KL, Wise DH (2000) *Pedobiologia* 44:33–39.
17. Lussenhop J (1992) *Adv Ecol Res* 23:1–33.
18. Toft S, Wise DH (1999) *Oecologia* 119:191–197.
19. Wise DH (2004) *Pedobiologia* 48:181–188.
20. Bengtsson G, Hedlund K, Rundgren S (1993) *Oecologia* 93:296–302.
21. Hasegawa M, Takeda H (1995) *Pedobiologia* 39:155–169.
22. Environmental Protection Agency (1998) *Climate Change and Kentucky* (Environmental Protection Agency, Washington, DC), Publication EPA236-F-98-007j.