

Florida State University Libraries

2015

Habitat Configuration Affects Spatial Pattern of \hat{I}^2 Diversity of Insect Communities Breeding in Oyster Mushrooms

Brian Inouye and Komei Kadowaki



Predator contributions to belowground responses to warming

A. M. MARAN AND S. L. PELINI†

Department of Biological Sciences, Bowling Green State University, Bowling Green, Ohio 43403 USA

Citation: Maran, A. M., and S. L. Pelini. 2016. Predator contributions to belowground responses to warming. *Ecosphere* 7(9):e01457. 10.1002/ecs2.1457

Abstract. Identifying the factors that control soil CO₂ emissions will improve our ability to predict the magnitude of climate change–soil ecosystem feedbacks. Despite the integral role of invertebrates in belowground systems, they are excluded from climate change models. Soil invertebrates have consumptive and nonconsumptive effects on microbes, whose respiration accounts for nearly half of soil CO₂ emissions. By altering the behavior and abundance of invertebrates that interact with microbes, invertebrate predators may have indirect effects on soil respiration. We examined the effects of a generalist arthropod predator on belowground respiration under different warming scenarios. Based on research suggesting invertebrates may mediate soil CO₂ emission responses to warming, we predicted that predator presence would result in increased emissions by negatively affecting these invertebrates. We altered the presence of wolf spiders (*Pardosa* spp.) in mesocosms containing a forest floor community. To simulate warming, we placed mesocosms of each treatment in ten open-top warming chambers ranging from 1.5° to 5.5°C above ambient at Harvard Forest, Massachusetts, USA. As expected, CO₂ emissions increased under warming and we found an interactive effect of predator presence and warming, although the effect was not consistent through time. The interaction between predator presence and warming was the inverse of our predictions: Mesocosms with predators had lower respiration at higher levels of warming than those without predators. Carbon dioxide emissions were not significantly associated with microbial biomass. We did not find evidence of consumptive effects of predators on the invertebrate community, suggesting that predator presence mediates response of microbial respiration to warming through nonconsumptive means. In our system, we found a significant interaction between warming and predator presence that warrants further research into mechanism and generality of this pattern to other systems.

Key words: brown food web; carbon; climate change; invertebrate; predator; soil respiration; warming.

Received 26 May 2016; **accepted** 9 June 2016. Corresponding Editor: D. P. C. Peters.

Copyright: © 2016 Maran and Pelini. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** spelini@bgsu.edu

INTRODUCTION

Understanding what controls the rate of CO₂ release from the soil is imperative if we are to predict future climate change. Soil carbon emissions account for ten times more CO₂ release than anthropogenic inputs, and the potential for positive climate–soil carbon emission feedbacks makes identifying the mechanisms behind soil carbon emissions important (Schlesinger and Andrews 2000, IPCC 2013). Currently, Earth System Models (ESMs) used to predict climate change include only microbial and plant respiration in

calculations of soil CO₂ emissions (Wieder et al. 2013). This approach fails to take into account the complexity of soil food webs, which are comprised largely of invertebrates that control microbe and plant dynamics. Soil invertebrates are omitted from ESMs because their direct contribution to soil respiration is trivial relative to that of plant roots (~45% of total soil respiration) and microbes (~55% of total soil respiration) (Lavelle 1997, Hanson et al. 2000, Schlesinger and Andrews 2000); however, invertebrates have significant indirect effects on soil carbon release, particularly through their role in the detrital food web.

By consuming microbes, invertebrates directly alter their abundance (reviewed in Wardle 2002) and suppress microbial response to warming (Crowther et al. 2015). Often, invertebrates feed selectively, altering microbe community structure (Ronn et al. 2002, Wardle 2006, Crowther et al. 2011), which may be important in determining soil CO₂ emissions (Strickland et al. 2009, De Vries et al. 2013). Strickland et al. (2009) suggest that microbe community structure may explain up to 20% variation of total carbon respiration.

Invertebrates affect the microbial community indirectly as well. For example, earthworms, ants, and millipedes act as “ecosystem engineers,” physically altering the soil environment through means such as burrowing, shredding detritus, and excreting labile carbon and nutrient sources, which are readily broken down by microbes (Lavelle 1997, Wardle 2006, Nielson et al. 2011, Del Toro et al. 2015). As soil microbes are restricted in their ability to move to new resources and they depend partly on invertebrates to provide new substrates, the activity of these ecosystem engineers stimulates microbes (Lavelle 1997, Rantalainen et al. 2004). In fact, the presence of invertebrates has been shown to contribute to increased soil respiration (Lavelle 1997, Fox et al. 2006, De Vries et al. 2013, Del Toro et al. 2015, Pelini et al. 2015) and decomposition (Wall et al. 2008), particularly in systems not constrained by temperature or precipitation (e.g., temperate and wet tropical biomes).

The responses of soil invertebrates to warming are varied. A meta-analysis by Blankinship et al. (2011) suggests that differences between studies may be explained by the climate where the study was conducted and from which the study organisms originated. In colder and drier climates, Blankinship et al. found stronger negative effects on invertebrate abundances, and these effects were more likely to be observed in long-term experiments. This meta-analysis focused on changes in abundance, but not community structure, under warming. Warming has been shown to change invertebrate community structure (Bokhorst et al. 2008, Briones et al. 2009, Zhang et al. 2013, Pelini et al. 2014), and as with microbes, a change in invertebrate community structure may alter ecosystem functioning (Heemsbergen et al. 2004). Changes in invertebrate and/or microbial community structure are

particularly important when they result in reductions in functional diversity, as more variation in functional roles can lead to facilitative interactions that promote decomposition (Heemsbergen et al. 2004). In addition, the presence of invertebrates that selectively graze on fungi has been shown to prevent warming effects on fungi (A’Bear et al. 2013) suggesting that community structure could determine the role of invertebrates in mediating ecosystem responses to warming.

Yet, soil invertebrate responses to warming, and the consequent effects on microbes and soil respiration, may be driven by predators, such as wolf spiders. By consuming detritivores and microbivores, predators exert top-down control on microbes (Gessner et al. 2010), and therefore have cascading effects on soil respiration. Further, by selectively grazing, predators may alter invertebrate community structure (Gessner et al. 2010). However, indirect effects of predator presence on invertebrate behavior have been shown to be equal to or greater than direct consumptive effects (Preisser et al. 2005, Strickland et al. 2013, reviewed in Sitvarin et al. 2016). Indeed, there is evidence of predator presence having far-reaching effects, including on rates of decomposition (Hawlena et al. 2012), soil respiration (Sitvarin and Rypstra 2014), and plant biomass (Zhao et al. 2013). These indirect effects of predators may be even more important under climate change as warming has been shown to amplify the top-down effects of predators (Barton et al. 2009, Jochum et al. 2012).

The objective of this study was to determine the contributions of soil invertebrate predators to soil respiration under different warming scenarios, with a focus on the detrital part of the belowground food web. We expected increased predator activity under warming to reduce microbivore abundance and stimulate a fear response (e.g., burrowing) in soil invertebrates. Due to this reduction in microbivores and increased activity of detritivores, we hypothesized that predator presence would amplify the increase of soil respiration under warming. To test the hypothesis, we altered the presence of wolf spiders (*Pardosa* spp.) in mesocosms containing soil fauna. Warming was simulated by placing mesocosms of each treatment in 10 open-top warming chambers ranging from 1.5° to 5.5°C above ambient at Harvard Forest, Massachusetts, USA.

METHODS

Study site

We placed mesocosms (30 cm diameter × 44 cm height) in 5 m diameter, open-top warming chambers at Harvard Forest, Petersham, Massachusetts, USA, which had been running for 5 yr prior to this experiment. The temperature inside each chamber is raised a set level above the ambient temperature via a forced air system. Warming levels were at 0.5°C increments from 1.5° to 5.5°C above ambient, which resulted in 10 warming treatments. For a detailed explanation of how the heating system works, see Pelini et al. (2011).

Mesocosm construction

We constructed the mesocosms using 18.9-L plastic buckets (Encore, Sandusky, Ohio, USA). To ensure similar drainage capability in all buckets, we used a template to drill seven, evenly spaced, 4 mm diameter holes in the bottom of each bucket. After the holes were drilled, we placed 5200 mL of sand (purchased from Gelinas, Orange, Massachusetts, USA) into each bucket, creating a layer approximately 10 cm high. The sand facilitated drainage and acted as a barrier between the ground and the soil layers in the mesocosms. To replicate the natural soil horizons, we added a 5200-mL mineral soil layer (B horizon, Canton loam), followed by a 5200-mL organic soil layer (O and A horizons, Canton loam). We collected the soil near to the warming chambers and used the cone-and-quarter method (Gerlach et al. 2002) to separately homogenize the organic soil, mineral soil, and sand. After homogenization, we removed macroscopic invertebrates (e.g., ants, worms). We planted one red maple (*Acer rubrum*) sapling (15–25 cm in height) (Musser Forests, Indiana, Pennsylvania, USA) in each bucket and allowed the planted mesocosms to acclimate in a greenhouse for 5 d. However, due to high mortality (72%) 4 weeks into the experiment we cut all saplings at the soil level to ensure that all mesocosms were under similar conditions.

We added invertebrates in densities representative of the forest floor surrounding the warming chambers. Three juvenile millipedes (Diplopoda), three earthworms (Megadrilacea, observed to be epigeic), and 45 mL of homogenized, fine leaf litter containing approximately 20 springtails (Collembola) and 14 mites (Acari)

were added to each mesocosm. The fine litter was obtained by sieving litter that was collected from litter baskets near to the warming chambers. Sieving removed all large invertebrates, but left densities of springtails and mites similar to natural densities. After homogenization, we verified nearly equal densities of springtails and mites throughout by counting several subsamples. Although we did not remove springtails or mites from the soil added to the mesocosms, the density in the soil was low (on average 3 per 50 mL), creating a need to supplement with this leaf litter community. We added two wolf spiders (*Pardosa* sp.) to half of the mesocosms (predator treatment). The escape or addition of new invertebrates to the mesocosms over the course of the experiment was prevented by a 1 mm mesh fabric covering the whole mesocosm, and tied with a rubber band to allow access during measurements. Finally, to mimic natural forest floor settings, we placed 2 g of dried leaf litter, collected from litter baskets near to the chambers, in each mesocosm.

Experimental design

Treatments involved the manipulation of predator presence (two levels) and temperature (one control and nine warming chambers), resulting in 20 treatments. We replicated each treatment three times, for a total of 60 mesocosms. CO₂ efflux was measured weekly in each mesocosm using a LI-6400 (LI-COR, Lincoln, Nebraska, USA) within a 10 cm diameter, 4.5 cm high PVC collar inserted 1 cm into the soil. The LI-6400 recorded three efflux readings during each measurement, which were averaged to produce one efflux reading for the mesocosm on that measurement day. Three times a week, we collected soil water from 10 cm long, 2.5 mm diameter microlysimeters (rhizon samplers; Soil Moisture, Santa Barbara, California, USA) that were inserted into the soil. There were several instances where we could not collect enough soil solution for analysis, but it did not consistently occur in one mesocosm and was likely due to improperly sealed vacuette tubes used for collecting the solution from the microlysimeters. The concentration of NO₃⁻, NH₄⁺, and total free primary amines in the soil solution samples collected from the microlysimeters was determined using fluorometric and colorimetric methods described in Darrouzet-Nardi and

Weintraub (2014) and analyzed on a Shimadzu TOC-V_{CPN} analyzer (Shimadzu Scientific Instruments, Columbia, Maryland, USA).

We harvested the mesocosms at two different time points, one replicate of each treatment on 7 October 2014, 5 weeks after the experiment began, and the remaining two replicates of each treatment on 9 October 2014, 10 weeks after the experiment began. At each harvest, we destructively sampled mesocosms for invertebrate soil depth, invertebrate mortality, and microbial biomass. The harvest of the buckets took place at the research site, directly outside the chambers.

Microbial biomass (C and N) was determined by fumigation–extraction, using the protocol described by Weintraub et al. (2007). We added 0.5 mol/L potassium sulfate (K₂SO₄) to 5 g of homogenized soil from each mesocosm and mixed the soil on a shaker table at 120 rpm for 1 h. After shaking, we vacuum-filtered the samples through Pall A/E glass fiber filters and froze the extract at –18°C. Alongside the K₂SO₄ extraction, we fumigated 5 g of homogenized soil by adding two milliliters of chloroform and incubating the samples for 24 h, followed by 30 min of venting. They were extracted using the same process described previously. The extracts were analyzed for DOC on a Shimadzu TOC-V_{CPN} analyzer. We subtracted dissolved organic carbon (DOC) in the unfumigated samples and controls from the DOC in fumigated samples to determine microbial biomass carbon. This process was repeated for dissolved organic nitrogen (DON) to determine microbial biomass nitrogen.

Data analysis

All analyses were carried out in R (R Core Team 2013) using the nlme package (Pinheiro et al. 2015). Using a linear mixed-effects model (LME), we regressed predator presence, warming, and their interaction against CO₂ efflux. We calculated warming by finding the mean temperature of the chamber (measured hourly), over the course of the experiment and subtracting the mean temperature of the control chamber. Efflux and nutrient (NO₃⁻, NH₄⁺, and total N) data were log-transformed. We accounted for mesocosm and chamber effects by nesting mesocosm within chamber as a random effect. An autoregressive correlation structure of order 1 described the autocorrelation of weekly efflux measurements

taken from the same mesocosm. Once we established the random-effects structure, we used backwards model selection with Wald *F* tests to determine the best fixed-effects structure (Bolker et al. 2009, Zuur et al. 2009).

We used the same process to explore the effect of warming and predator presence on microbial biomass using LME, but with mesocosm and chamber nested within harvest date as a random effect to account for the effect of the harvest date. Additionally, we looked at the effect of microbial biomass on the final efflux measurement before harvest. As microbial biomass was only measured during harvest, using the final efflux measurement was necessary because it is unlikely that microbial biomass would remain stable throughout the experiment and therefore could predict only the last efflux reading. Using the same LME model structure, we looked at the effect of invertebrate density on the last efflux reading. We used a permutational multivariate analysis of variance (PERMANOVA) in the VEGAN package in R (Oksanen et al. 2015) to look at the effects of warming and predator presence on the invertebrate community.

We determined the effects of warming, predator presence, and their interaction on respiration for three different time periods, using three separate models. One model was created for the first four weeks, before the first harvest, using the data for all mesocosms (hereafter “preharvest model”); another model incorporated data for only the two replicates remaining after the first harvest, from five weeks until the end of the experiment (hereafter “postharvest model”). A third model incorporated data for all mesocosms throughout the entire experiment (hereafter “full experiment model”). We partitioned the data in this way for two reasons: Mesocosm experiments require stabilization periods, with effects only evident after some time has passed (Sitvarin and Rypstra 2014, Pelini et al. 2015), and shortly after the first harvest, the plants were removed (see “Mesocosm construction”). We could have included time as a fixed effect in a full experiment model, but since after the first harvest one replicate was removed, the change in sample size may have given more weight to the preharvest measurements where the plant was present and mesocosms were not yet stabilized. Using the method described above, we used a LME to determine whether the state of the plant (alive/dead)

had an effect on soil nutrients. No effect on the soil nutrients would suggest that plant death did not greatly alter processes in the mesocosms. We also considered total N and total reducing sugars as possible predictors for efflux; however, we had to use separate models from those described above as the data set including nutrients is smaller (60% the size of the full data set) due to difficulties encountered during soil water extraction (see *Experimental design*). As we measured nutrients throughout the whole experiment, this nutrient data subset is most similar to the one used in the “full experiment model,” but with fewer data points. Because of the similarity to the full experiment data set, we would expect similar findings of predator presence and warming on efflux, but can gain insight into the effect of nutrients on efflux through this analysis. We calculated marginal and conditional R^2 for each LME model using the methods described by Nakagawa and Schielzeth (2013). Marginal R^2 is the proportion of the variance explained by only the fixed effects, while conditional R^2 is the proportion of the variance explained by both the fixed and random effects.

RESULTS

During the preharvest period and for data taken from the full experiment, CO₂ efflux was

Table 1. Results of the Wald F test to determine significance of fixed effects in the linear mixed-effects models.

Fixed effect removed	Δ AIC	Wald F	P
Preharvest model			
Warming:Predator	3.8	1.74	0.19
Warming	0.8	0.08	0.78
Predator	1.1	0.91	0.34
Postharvest model			
Warming:Predator	-4.3	6.68	0.012
Full experiment model			
Warming:Predator	0.23	1.78	0.19
Warming	1.7	0.31	0.59
Predator	1.9	0.05	0.82
Nitrogen subset model			
Warming:Nitrogen	1.4	1.45	0.23
Predator:Nitrogen	1.1	2.16	0.14
Warming:Predator	2.6	0.34	0.56
Predator	1.6	0.42	0.52
Warming	-0.2	0.14	0.71
Nitrogen	-3.8	9.75	0.002

Note: AIC, Akaike information criterion.

not significantly predicted by warming, predator presence, their interaction, or any other explanatory variables considered in this study (Table 1). However, during the postharvest period, the best fit model of CO₂ efflux included warming, predator presence, and their interaction ($F = 6.68$, $df = 8$, $P = 0.012$; marginal $R^2 = 0.06$, conditional $R^2 = 0.16$). When predators were absent, CO₂ efflux increased with warming. However, when predators were present, CO₂ efflux did not increase with warming (Fig. 1, Tables 1 and 2).

Efflux was not predicted by total reducing sugars or NH₄. However, it was significantly predicted by total N ($F = 9.75$, $df = 6$, $P = 0.002$; marginal $R^2 = 0.04$, conditional $R^2 = 0.06$; Fig. 2) and NO₃, which makes up ~45% of total N ($F = 9.11$, $df = 8$, $P < 0.0028$; marginal $R^2 = 0.06$, conditional $R^2 = 0.07$; Fig. 3, Table 1), but not warming, predator presence, or their interaction. Over the course of the experiment, efflux decreased ($F = 287.61$, $df = 6$, $P < 0.0001$; marginal $R^2 = 0.36$, conditional $R^2 = 0.44$; Fig. 4). Warming, predator presence, and their interaction did not predict NO₃, total

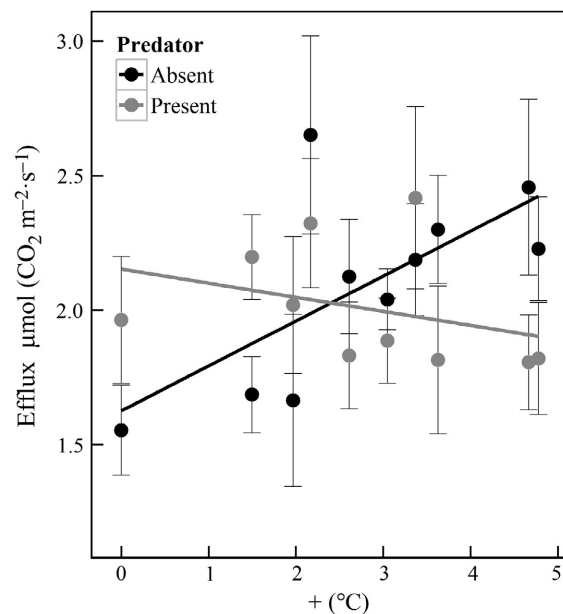


Fig. 1. Soil CO₂ efflux as predicted by level of warming above ambient temperature, wolf spider presence, and their interaction during postharvest time period ($P = 0.012$, marginal $R^2 = 0.06$, conditional $R^2 = 0.16$). Each point represents the average efflux measured during the postharvest period \pm SE.

Table 2. Summary of fixed effects of the postharvest model.

Fixed effect	Coefficient	SE	df
Warming	0.09	0.03	8
Predator	0.29	0.14	28
Warming:Predator	-0.12	0.05	28

N, or reducing sugars. Death of the plant did not significantly affect total reducing sugars, total N, NO_3^- , or NH_4^+ , but efflux did decrease after plant death ($F = 67.5$, $df = 6$, $P < 0.0001$; marginal $R^2 = 0.09$, conditional $R^2 = 0.10$; Fig. 5).

Microbial biomass, invertebrate community, and earthworm burrowing depth at harvest were not predicted by warming, predator presence, or their interaction. The efflux measurement taken just before harvest was not predicted by microbial biomass or invertebrate density.

DISCUSSION

CO_2 efflux was significantly correlated with warming, predator presence, and their interaction during the last 5 weeks of the experiment. Contrary to our prediction, when predators were

present, CO_2 efflux did not increase under warming as it did in the absence of predators. Although the relationship was not strongly predictive, this finding suggests that predator presence may impact the effect of warming on detrital food webs and soil ecosystem functioning.

We hypothesized that predators would alter belowground response to warming by both reducing the abundance of and eliciting a fear response in the soil invertebrates that consume and/or alter resource availability for microbes. We did not find an effect of predators or warming on invertebrate abundance or microbial biomass C, which suggests that predators did not reduce CO_2 via greater consumption, but rather through a nonconsumptive pathway. Although we do not have data to draw conclusions about the invertebrates' behavioral response to predator presence, there is evidence of nonconsumptive predator effects on these taxa, particularly springtails, in other studies (Zhao et al. 2013, Sitvarin and Rypstra 2014). Because springtail presence is generally associated with increased soil respiration (Fox et al. 2006), their altered activity could result in a reduction of CO_2 efflux. Indeed, a recent study by Sitvarin and Rypstra (2014) found that fear of predation by wolf spiders

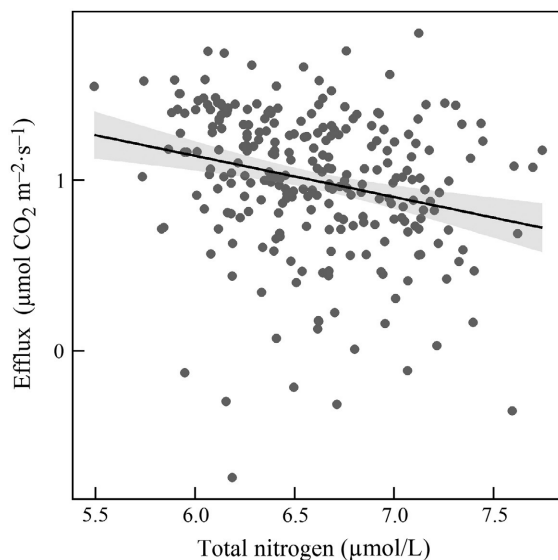


Fig. 2. Soil CO_2 efflux as predicted by total nitrogen (including NH_4^+ , NO_3^- , and total free primary amines) measured in soil solution ($P < 0.01$, marginal $R^2 = 0.04$, conditional $R^2 = 0.06$). The trend line is surrounded by a 0.95 confidence interval.

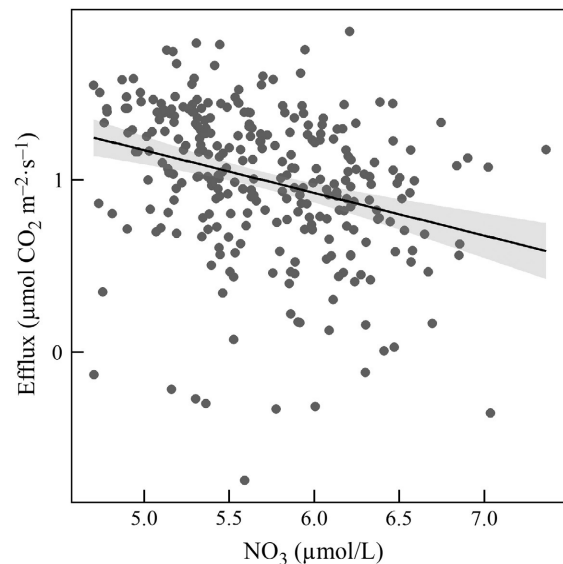


Fig. 3. Soil CO_2 efflux as predicted by NO_3^- measured in soil solution ($P < 0.0001$, marginal $R^2 = 0.06$, conditional $R^2 = 0.07$). NO_3^- drives the inverse relationship between efflux and total nitrogen (Fig. 2). The trend line is surrounded by a 0.95 confidence interval.

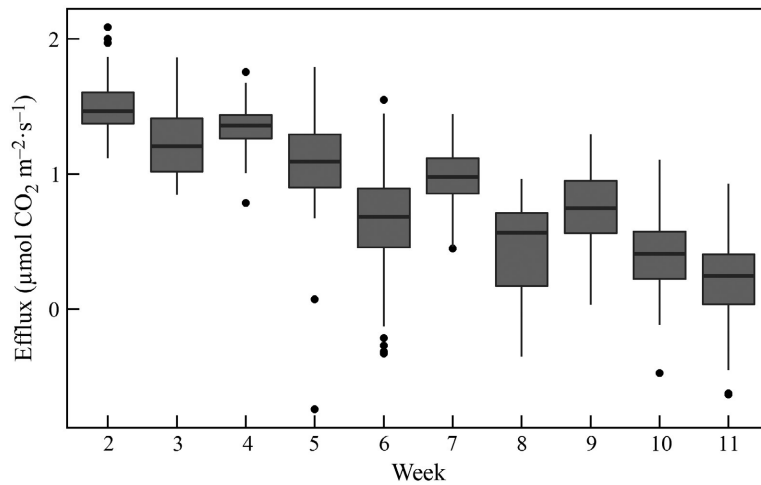


Fig. 4. Soil CO₂ efflux over time for all mesocosms, not separated by treatment ($P < 0.0001$, marginal $R^2 = 0.36$, conditional $R^2 = 0.44$).

(also *Pardosa* sp.) drove CO₂ efflux decreases likely because springtail activity decreases in the presence of predators (also see Nilsson and Bengtsson 2004). In addition, if soil invertebrates are shifting their food preference when predators are present, as has been observed in other systems (Schmitz 2006, Schmitz et al. 2010), the microbe community structure may have changed (Ronn et al. 2002, Wardle 2006, Crowther et al. 2011), which can impact CO₂ efflux (Strickland et al. 2009). The interaction between predator presence and warming observed in this study could result if warming increased activity of the spiders and/or invertebrates (Chown and Nicolson 2004), leading to more predator–prey encounters and the amplification of nonconsumptive effects.

The contributions of predator presence to CO₂ efflux responses to warming varied through time. The relationship is only apparent after week five, during the postharvest time period. This may be due to mesocosm stabilization or the plants' presence masking predator and warming effects during the preharvest time period. Most plants died within a reasonable range of time when the mesocosms may have been stabilizing (Pelini et al. 2015). The shared timing of these events makes drawing conclusions about why the pattern did not emerge until week five difficult, although the drop in efflux after plant death (Fig. 5) suggests that plant root respiration was masking soil microbial respiration differences between treatments. With roots no longer

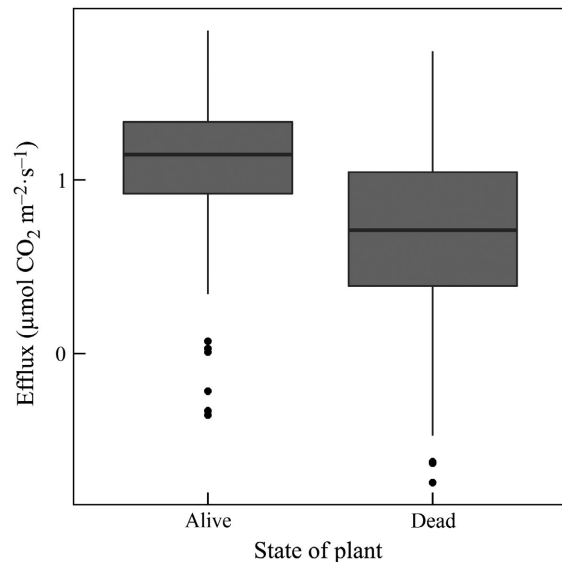


Fig. 5. Soil CO₂ efflux by the state of the plant for all mesocosms, not separated by treatment ($P < 0.0001$, marginal $R^2 = 0.09$, conditional $R^2 = 0.10$). Plant state was assessed qualitatively, making judgments based on number of healthy leaves left and overall appearance.

releasing CO₂ upon plant death, the effects of predator presence and warming on microbial CO₂ release would be more apparent. It is also possible that the death of the plant may have changed the microclimate in the mesocosm, or reduced substrate for microbes, as plant roots

and their exudates provide material to microbes for break down (Newman and Watson 1977, Lavelle 1997).

When looking at a subset of the data that included only those dates with enough dissolved nutrient solution for analysis, which used similar data to the “full experiment model,” we found that total N (driven mostly by NO_3^-), but not warming or predator presence, was negatively related to soil CO_2 efflux (Fig. 3). This may be due to “carbon starvation” (Weintraub et al. 2007): Carbon was likely abundant in the mesocosms at the beginning of the experiment, but with no new inputs, carbon may have become less available, which would have resulted in lower soil CO_2 efflux over time (Fig. 4) and possibly higher N mineralization (Clarholm 1985, Weintraub et al. 2007). Due to the number of weeks we were unable to obtain enough soil solution to measure soil nutrients, this data set is not large enough to look at different time periods, which makes it difficult to determine how important nitrogen was during the postharvest period when we saw an effect of predator presence and warming on efflux. Even considering these challenges, the interaction between predation and warming is highly significant and likely not spurious.

This study provides insight into the role of soil invertebrates in the carbon cycle, the extent of which is not yet known and is in need of further research (Schmitz et al. 2014). The results suggest that generalist invertebrate predators may reduce CO_2 efflux in detrital food webs under warming, which aligns well with other studies that have found soil invertebrates may overwhelm the response of microbes to warming (Crowther et al. 2015, Pelini et al. 2015). Our findings cannot be used to directly improve climate models due to their low predictive power; however, they could have implications for climate change mitigation strategies. Conservation efforts that work to maintain complete detrital food webs in deciduous forests could reduce soil CO_2 efflux, reducing feedback effects of climate change and warming. Protecting predators is particularly important as higher trophic levels are more sensitive to warming (Menge and Sutherland 1987, Voigt et al. 2003, Preisser and Strong 2004). The results of this study warrant future research into mechanistic explanations and generality of the effect to other systems.

ACKNOWLEDGMENTS

We thank Heather Clendenin, Laura Figueroa, Robby Baroudi, Michael Pelini, Paul Best, William Werner, Matthew Lau, Katie Miller, and Manisha Patel for field and laboratory assistance. Kevin McCluney provided guidance on design and statistical analysis. Michael Weintraub provided guidance, resources, and facilities for microbial biomass assays and soil solution nutrient analysis. We thank two anonymous reviewers for providing feedback that greatly improved our manuscript. We also thank Aaron Ellison, Rob Dunn, Nick Gotelli, and Nate Sanders for the use of the warming chambers funded by the U.S. Department of Energy for Ecosystem Research (DE-FG02-08ER64510) and NSF DOB (1136703). Funding was provided by the Building Strength Program at Bowling Green State University, Sigma Xi Grants-in-Aid of Research (G20141015641995), and the U.S. National Science Foundation Research Experiences for Undergraduates (DBI 1459519) award to Harvard Forest.

LITERATURE CITED

- A'Bear, A. D., L. Boddy, and T. H. Jones. 2013. Bottom-up determination of soil collembola diversity and population dynamics in response to interactive climatic factors. *Oecologia* 173:1083–1087.
- Barton, B. T., A. P. Beckerman, and O. J. Schmitz. 2009. Climate warming strengthens indirect interactions in an old-field food web. *Ecology* 90:2346–2351.
- Blankinship, J. C., P. A. Niklaus, and B. A. Hungate. 2011. A meta-analysis of responses of soil biota to global change. *Oecologia* 165:553–565.
- Bokhorst, S., A. Huiskes, P. Convey, P. M. van Bodegom, and R. Aerts. 2008. Climate change effects on soil arthropod communities from the Falkland Islands and the Maritime Antarctic. *Soil Biology and Biochemistry* 40:1547–1556.
- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24:127–135.
- Briones, M. J. I., N. J. Ostle, N. R. McNamara, and J. Poskitt. 2009. Functional shifts of grassland soil communities in response to soil warming. *Soil Biology and Biochemistry* 41:315–322.
- Chown, S., and S. Nicolson. 2004. Insect physiological ecology: mechanisms and patterns. Oxford University Press, Oxford, UK.
- Clarholm, M. 1985. Interactions of bacteria, protozoa and plants leading to mineralization of soil-nitrogen. *Soil Biology and Biochemistry* 17:181–187.

- Crowther, T. W., T. H. Jones, and L. Boddy. 2011. Species-specific effects of grazing invertebrates on mycelial emergence and growth from woody resources into soil. *Fungal Ecology* 4:333–341.
- Crowther, T. W., S. M. Thomas, D. S. Maynard, P. Baldrian, K. Covey, S. D. Frey, L. T. A. van Diepen, and M. A. Bradford. 2015. Biotic interactions mediate soil microbial feedbacks to climate change. *Proceedings of the National Academy of Sciences USA* 112:7033–7038.
- Darrouzet-Nardi, A., and M. N. Weintraub. 2014. Evidence for spatially inaccessible labile N from a comparison of soil core extractions and soil pore water lysimetry. *Soil Biology and Biochemistry* 73:22–32.
- De Vries, F. T., et al. 2013. Soil food web properties explain ecosystem services across European land use systems. *Proceedings of the National Academy of Sciences USA* 110:14296–14301.
- Del Toro, I., R. R. Ribbons, and A. M. Ellison. 2015. Ant-mediated ecosystem functions on a warmer planet: effects on soil movement, decomposition and nutrient cycling. *Journal of Animal Ecology* 84:1233–1241.
- Fox, O., S. Vetter, K. Ekschmitt, and V. Wolters. 2006. Soil fauna modifies the recalcitrance-persistence relationship of soil carbon pools. *Soil Biology and Biochemistry* 38:1353–1363.
- Gerlach, R. W., D. E. Dobb, G. A. Raab, and J. M. Nocerino. 2002. Gy sampling theory in environmental studies. 1. Assessing soil splitting protocols. *Journal of Chemometrics* 16:321–328.
- Gessner, M. O., C. M. Swan, C. K. Dang, B. G. McKie, R. D. Bardgett, D. H. Wall, and S. Hattenschwiler. 2010. Diversity meets decomposition. *Trends in Ecology and Evolution* 25:372–380.
- Hanson, P. J., N. T. Edwards, C. T. Garten, and J. A. Andrews. 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* 48: 115–146.
- Hawlena, D., M. S. Strickland, M. A. Bradford, and O. J. Schmitz. 2012. Fear of predation slows plant-litter decomposition. *Science* 336:1434–1438.
- Heemsbergen, D. A., M. P. Berg, M. Loreau, J. R. van Haj, J. H. Faber, and H. A. Verhoef. 2004. Biodiversity effects on soil processes explained by interspecific functional dissimilarity. *Science* 306: 1019–1020.
- IPCC. 2013. *Climate change 2013: the physical science basis. Working group I contribution to the fifth assessment report of the intergovernmental panel on climate change.* IPCC, Cambridge, UK.
- Jochum, M., F. D. Schneider, T. P. Crowe, U. Brose, and E. J. O’Gorman. 2012. Climate-induced changes in bottom-up and top-down processes independently alter a marine ecosystem. *Philosophical Transactions of the Royal Society B* 367:2962–2970.
- Lavelle, P. 1997. Faunal activities and soil processes: adaptive strategies that determine ecosystem function. *Advances in Ecological Research* 27: 93–132.
- Menge, B. A., and J. P. Sutherland. 1987. Community regulation-variation in disturbance, competition, and predation in relation to environmental-stress recruitment. *American Naturalist* 130:730–757.
- Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- Newman, E. I., and A. Watson. 1977. Microbial abundance in rhizosphere-computer-model. *Plant and Soil* 48:17–56.
- Nielson, U. N., E. Ayres, D. H. Wall, and R. D. Bardgett. 2011. Soil biodiversity and carbon cycling: a review and synthesis of studies examining diversity-function relationships. *European Journal of Soil Science* 62:105–116.
- Nilsson, E., and G. Bengtsson. 2004. Death odour changes movement pattern of a Collembola. *Oikos* 104:509–517.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O’Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2015. *vegan: community Ecology Package.* R package version 2.2-1. <http://CRAN.R-project.org/package=vegan>
- Pelini, S. L., F. P. Bowles, A. M. Ellison, N. J. Gotelli, N. J. Sanders, and R. R. Dunn. 2011. Heating up the forest: open-top chamber warming manipulation of arthropod communities at Harvard and Duke Forests. *Methods in Ecology and Evolution* 2: 534–540. <http://dx.doi.org/10.1111/j.2041-210X.2011.00100.x>
- Pelini, S. L., S. E. Diamond, L. M. Nichols, K. L. Stuble, A. M. Ellison, N. J. Sanders, R. R. Dunn, and N. J. Gotelli. 2014. Geographic differences in effects of experimental warming on ant species diversity and community composition. *Ecosphere* 5:art125.
- Pelini, S. L., A. M. Maran, A. Chen, J. Kaseman, and T. W. Crowther. 2015. Higher trophic levels overwhelm climate change impacts on terrestrial ecosystem functioning. *PLoS One* 10:e0136344.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2015. *nlme: linear and nonlinear mixed effects models.* R package version 3.1-128. <http://CRAN.R-project.org/package=nlme>
- Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86:501–509.

- Preisser, E. L., and D. R. Strong. 2004. Climate affects predator control of an herbivore outbreak. *American Naturalist* 163:754–762.
- R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Rantalainen, M. L., H. Fritze, J. Haimi, O. Kiikkila, T. Pennanen, and H. Setälä. 2004. Do enchytraeid worms and habitat corridors facilitate the colonisation of habitat patches by soil microbes? *Biology and Fertility of Soils* 39:200–208.
- Ronn, R., A. E. McCaig, B. S. Griffiths, and J. I. Prosser. 2002. Impact of protozoan grazing on bacterial community structure in soil microcosms. *Applied and Environmental Microbiology* 68:6094–6105.
- Schlesinger, W. H., and J. A. Andrews. 2000. Soil respiration and the global carbon cycle. *Biogeochemistry* 48:7–20.
- Schmitz, O. J. 2006. Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. *Ecology* 87:1432–1437.
- Schmitz, O. J., D. Hawlena, and G. C. Trussell. 2010. Predator control of ecosystem nutrient dynamics. *Ecology Letters* 13:1199–1209.
- Schmitz, O. J., et al. 2014. Animating the carbon cycle. *Ecosystems* 17:344–359.
- Sitvarin, M. I., and A. L. Rypstra. 2014. Fear of predation alters soil carbon dioxide flux and nitrogen content. *Biology Letters* 10:4.
- Sitvarin, M. I., A. L. Rypstra, and J. Harwood. 2016. Linking the green and brown worlds through nonconsumptive predator effects. *Oikos*. <http://dx.doi.org/10.1111/oik.03190>
- Strickland, M. S., D. Hawlena, A. Reese, M. A. Bradford, and O. J. Schmitz. 2013. Trophic cascade alters ecosystem carbon exchange. *Proceedings of the National Academy of Sciences USA* 110:11035–11038.
- Strickland, M. S., C. Lauber, N. Fierer, and M. A. Bradford. 2009. Testing the functional significance of microbial community composition. *Ecology* 90:441–451.
- Voigt, W., et al. 2003. Trophic levels are differentially sensitive to climate. *Ecology* 84:2444–2453.
- Wall, D., et al. 2008. Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biology* 14:2661–2677.
- Wardle, D. A. 2002. *Communities and ecosystems: linking the aboveground and belowground components*. Princeton University Press, Princeton, New Jersey, USA.
- Wardle, D. A. 2006. The influence of biotic interactions on soil biodiversity. *Ecology Letters* 9:870–886.
- Weintraub, M. N., L. E. Scott-Denton, S. K. Schmidt, and R. K. Monson. 2007. The effects of tree rhizodeposition on soil exoenzyme activity, dissolved organic carbon, and nutrient availability in a sub-alpine forest ecosystem. *Oecologia* 154:327–338.
- Wieder, W. R., G. B. Bonan, and S. D. Allison. 2013. Global soil carbon projections are improved by modelling microbial processes. *Nature Climate Change* 3:909–912.
- Zhang, S. X., Q. Li, Y. Lu, X. P. Zhang, and W. J. Liang. 2013. Contributions of soil biota to C sequestration varied with aggregate fractions under different tillage systems. *Soil Biology and Biochemistry* 62:147–156.
- Zhao, C., J. N. Griffin, X. Wu, and S. Sun. 2013. Predatory beetles facilitate plant growth by driving earthworms to lower soil layers. *Journal of Animal Ecology* 84:749–758.
- Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer-Verlag, New York, New York, USA.