Higher Trophic Levels Overwhelm Climate Change Impacts on Terrestrial Ecosystem Functioning

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Abstract

Forest floor food webs play pivotal roles in carbon cycling, but they are rarely considered in models of carbon fluxes, including soil carbon dioxide emissions (respiration), under climatic warming. The indirect effects of invertebrates on heterotrophic (microbial and invertebrate) respiration through interactions with microbial communities are significant and will be altered by warming. However, the interactive effects of invertebrates and warming on heterotrophic respiration in the field are poorly understood. In this study we combined field and common garden laboratory approaches to examine relationships between warming, forest floor food web structure, and heterotrophic respiration. We found that soil animals can overwhelm the effects of warming (to 5 degrees Celsius above ambient) on heterotrophic respiration. In particular, the presence of higher trophic levels and burrowing detritivores strongly determined heterotrophic respiration rates in temperate forest soils. These effects were, however, context-dependent, with greater effects in a lower-latitude site. Without isolating and including the significant impact of invertebrates, climate models will be incomplete, hindering well-informed policy decisions.

Introduction

There is a critical need to improve estimates of future soil CO2 emissions (soil respiration, Rs), which are 10× greater than those generated by the burning of fossil fuels [1], and the potential feedbacks of the emissions to climate change. The impacts of increasing temperatures on microbes, which, along with plant roots are the primary contributors to Rs, are included in determination of soil-climate change feedbacks [2–5]. While the direct contribution of other soil and litter-dwelling organisms (e.g., invertebrate detritivores, vertebrate predators) to the heterotrophic component of Rs (i.e., R44) is presumed to be small relative to that of microbes,
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the indirect effects of climate change on R11 through animal-microbe interactions have not been sufficiently explored. Indeed, the absence of soil animals, particularly invertebrates, has been highlighted as a major limitation to current climate and carbon cycling models and management practices [6–10].

Soil food webs are dominated by invertebrates, which govern decomposition rates and soil structure via their interactions with microbial communities [11–17]. Direct trophic effects of invertebrates can regulate microbial activity in some regions [18,19], but the indirect effects generally enhance microbial growth and respiration. That is, by shredding litter [15,17,20,21] and moving soil [11,12,22,23], invertebrate engineers have the potential to stimulate microbial growth and nutrient mineralization [24].

Temperate forests harbor a variety of organisms that also have the capacity to drive cascading effects on microbial activity. However, there is mixed support for top-down trophic cascades on R11 via invertebrate predation [25,26]. Best and Welsh [27] demonstrated that salamanders affect forest leaf litter retention by regulating invertebrate populations, but the impacts on microbes and R11 remain unknown. The potential for cascading effects on R11 needs to be explored further because multiple studies have shown that warming strengthens the effects of predators on lower trophic levels and nutrient cycling in other food webs [21,28,29].

Invertebrates are highly responsive to climatic change [reviewed in 30]. Because invertebrates are ectotherms, the rates and magnitudes of predation and engineering should increase with temperature, at least until thermal thresholds are exceeded or competitive interactions shift [31]. The effects of warming on invertebrate activity may be magnified if soil invertebrates increase movement throughout the soil [32]. Based on this pattern, our understanding of R11 responses to warming remains incomplete until we consider the indirect effects of warming mediated through invertebrates.

In this study we examined relationships between warming, forest floor food web structure, and R11. We combined field and common garden laboratory experiments to separate indirect from direct and individual from community structure responses to warming on R11. More specifically, using open-top warming chambers at Harvard Forest and Duke Forest, we evaluated the effects of (1) warming on food web structure-R11 interactions, (2) macroinvertebrate communities shaped by different warming scenarios on R11, and (3) soils and their associated microbial and smaller invertebrate communities (micro/mesofauna) shaped by different warming scenarios on R11. Because we placed the same number of animals in all warming chambers, the field experiment (1) allowed us to assess how behavioral or physiological responses to warming affected R11. In contrast, we did not manipulate fauna in the common garden experiments (2 and 3), allowing us to determine if communities—macroinvertebrates (2) or micro/mesofauna (3)—shaped by warming differ in R11 even when the direct effects of warming on R11 were removed.

Methods

Study System

Access to the Harvard Forest field sites was permitted by Harvard University, and Duke University granted access to the Duke Forest field site. Use of salamanders was reviewed and approved by Harvard University/Faculty of Arts & Sciences Standing Committee on the Use of Animals in Research & Teaching (IACUC), approved Animal Experimentation Protocol No. 12–16.

We used open-top warming chambers and forest floor communities within or near them at Duke Forest and Harvard Forest [33]. Each of these two sites is equipped with 12 chambers (5 m diameter): 3 are ambient controls while the remaining 9 are heated, through forced air
delivery, to different degrees ranging from 1.5–5.5°C above ambient air temperature. These chambers had been running for three years when we began this study.

Field mesocosms (Experiment 1)

We manipulated dominant components of the forest floor food webs within mesocosms (19 L buckets, 30 cm diameter, 44 cm height) placed in Harvard Forest warming chambers. We filled each mesocosm to 10 cm height with topsoil (O and A horizons, Canton loam) that we collected ~100–200 yards away from the chambers, from which we removed roots and macrofauna (e.g., beetles, ants, spiders, millipedes) via sieving (1mm mesh), and homogenized across all mesocosms.

Biota treatments included 1: no fauna present; 2: only micro/mesofauna present; 3: only macroinvertebrates present; 4: micro/mesofauna and macroinvertebrates present; and 5: micro/mesofauna, macroinvertebrates, and a vertebrate predator present. We removed micro- (e.g., fungi, bacteria) and meso- (e.g., mites, springtails) fauna (Treatments 1 & 3) by autoclaving soil described above at 120°C for 30 minutes. We used red back salamanders (*Plethodon cinereu*) as the top predator in this experiment (Treatment 4) because salamanders are the most abundant vertebrates in many forest ecosystems [34] and have been shown to impact nutrient cycles in deciduous forests [27]. For treatments that included macroinvertebrates (Treatments 3 & 4), we used ~1.5 g each of live earthworms (Megadrilacea), a common invertebrate engineer and food source for salamanders, and mealworms (Tenebrionidae), one of the most abundant macroinvertebrates in the warming chambers at the time of experimental setup.

Into each mesocosm, we also installed a 10 cm diameter, 4.5 cm high, PVC collar, inserted approximately 1 cm into the soil. Within these collars we collected weekly soil efflux (RH) measurements using a LiCor 6400 (Lincoln, Nebraska). We counted and weighed all surviving macroinvertebrates at the end of the experiment. Mesocosms were present in the chambers for 6 weeks during June-August 2013.

Common garden mesocosms (Experiments 2 & 3)

**Experiment 2: Macroinvertebrates.** We collected litter and organic soil cores (20 cm diameter, 5–8 cm depth) from open-top warming chambers at Harvard Forest and Duke Forest [see 33] in June. We extracted macroinvertebrates, which we identified to class or order, from these cores using 48 hr Berlese funnel extraction and hand removal. We placed these live extracted invertebrates into PVC mesocosms (8 cm diameter, 10 cm depth; herein “macrofauna mesocosms”) in Harvard Forest greenhouse facilities. Mesocosms contained sieved, homogenized organic soil collected adjacent to the warming chambers at Harvard Forest.

**Experiment 3: Micro/mesofauna.** We collected additional soil cores from Harvard Forest chambers to determine if soils, along with micro- and mesofauna, originating from different warming scenarios varied in R$_{14}$ when placed into common conditions. We extracted four organic soil cores (20 cm diameter, 5–8 cm depth) from each chamber and placed them into PVC mesocosms (8 cm diameter, 10 cm depth herein “micro/mesofauna mesocosms”) in Harvard Forest greenhouse facilities.

We have data from Harvard Forest macrofauna mesocosms for two weeks, Duke Forest macrofauna mesocosms for four weeks (Experiment 2), and Harvard Forest micro/mesofauna for six weeks (Experiment 3). From all mesocosms we collected weekly soil efflux (R$_{14}$) measurements and macroinvertebrate and microbial C biomass at the end of the experiment. We used a LiCor 6400 (Lincoln, Nebraska) for soil respiration measurements. We used chloroform fumigation to estimate microbial C [modified from 35].
Data analyses

Field Experiment. We used linear mixed effects modeling to determine if $R_H$ varied significantly with warming (difference between average air temperature in heated versus control chambers during the experiment), biota treatments (none; micro/mesofauna only; macroinvertebrates only; micro/mesofauna + macroinvertebrates; micro/mesofauna + macroinvertebrates + salamander), and their interactions with time or each other (fixed effects) in mesocosms (nested within chamber; random effect). We accounted for repeated measures by including a time correlation structure in the model.

For mesocosms with macroinvertebrates, we used linear mixed modeling to determine if biota treatment, warming, and/or their interaction (fixed effects) were significantly associated with macroinvertebrate mortality. For these mesocosms, we also regressed the final $R_H$ measurements against macroinvertebrate biomass.

Common garden experiments. We pooled across the four soil cores collected in each warming chamber to determine if inter-chamber variation in average air temperature and soil moisture (April 2010 to June 2013; herein ‘microclimate’) was associated with macroinvertebrate community structure. We used linear regression to determine if taxonomic richness or abundance, and PERMANOVA to determine if community composition, varied with chamber microclimate. We did not pool across soil cores for analyses of mesocosm $R_H$ because fauna extracted from each soil core were held in separate mesocosms from which $R_H$ was measured. We used linear mixed models to determine if $R_H$ varied with microclimate in warming chambers from which fauna were collected, microbial biomass (for micro/mesofauna mesocosms and Duke Forest macrofauna mesocosms), and abundance of common macroinvertebrates. We modeled mesocosm as a random effect and incorporated time into the correlation structure of our models to account for repeated measures.

We performed all analyses in R (version 3.0.2). We obtained P-values via likelihood ratio tests of full models compared to those lacking the effects of interest. All raw data are available on the Harvard Forest data archive [36].

Results

Field experiment

The effect of the biota treatments on $R_H$ varied with time ($L(15) = 21; P = 0.001$). In the first week of the experiment, $R_H$ was highest in micro/mesofauna removal mesocosms, but in later weeks $R_H$ in these mesocosms was lower than that in the other mesocosms (Fig 1). Warming and its interactions with biotic treatment or time were not significant predictors of $R_H$.

The impact of warming on macroinvertebrate mortality varied with biota treatment ($L(7) = 9.5; P = 0.009$). More specifically, macroinvertebrate mortality did not vary with warming when micro/mesofauna and salamander predators were absent. However, the addition of micro/mesofauna yielded a strong positive association of warming and invertebrate mortality, but only when salamanders were not present (Fig 2).

Common garden

We extracted Araneae (spiders), Diplopoda (millipedes), Chilopoda (centipedes), Diptera (fly larvae), Coleoptera (beetles), Formicidae (ants), Lepidoptera (caterpillars), and Megadrilacea (earthworms) from Duke Forest and Harvard Forest warming chamber soil cores. Additionally, we collected Gastropoda (slugs) and Opiliones (Harvestmen) from Harvard Forest cores. Macroinvertebrate taxonomic richness and abundance did not vary significantly with microclimate in Duke Forest ($F_{2,0} = 0.16, p = 0.85$) or Harvard Forest ($F_{2,9} = 4.48, p = 0.067$) warming...
chambers. Community composition was not strongly associated with microclimate at either site (PERMANOVA: HFtemperature $F_{1,7} = 0.55, P = 0.73$; HFmoisture $F_{1,7} = 0.89, P = 0.50$; DFtemperature $F_{1,9} = 1.1, P = 0.39$; DFmoisture $F_{1,9} = 1.6, P = 0.17$; Fig 3).

RH of micro/mesofauna mesocosms from Harvard Forest warming chambers did not vary significantly with microclimate of origin or microbial biomass (temperature: $L(7) = 0.021, p = 0.89$; microbial biomass: $L(7) = 0.26, p = 0.61$; moisture: $L(7) = 0.61, p = 0.44$). Similarly, RH of macrofauna mesocosms from Harvard Forest warming chambers did not vary significantly with any microclimate or fauna parameters (Table 1). In contrast, RH of macrofauna mesocosms from Duke Forest increased significantly with abundance of millipedes and microbial biomass (Table 2).

**Discussion**

Our study highlights the prominent role of soil communities in the functioning of temperate forest ecosystems. In particular, it shows how initial differences in soil communities can overwhelm the direct effects of climate change on carbon exchanges between terrestrial and atmospheric pools. These effects were, however, context-dependent, with greater effects in a lower-latitude site. The context-dependent effects of soil fauna are consistent with the results of a previous global litter decomposition study [21], and highlight that the strength of the link between
soil communities and nutrient cycling is likely to increase at lower latitudes, where activity levels are not limited by temperature or moisture availability.

The primary drivers of the changes in RH were the epigeic (litter dwelling) and endogeic (burrowing) macrodetritivores (i.e., millipedes, earthworms). Via the comminution of litter and the mixing of soil, these taxa are known to influence the activity of soil microbes and stimulate the mineralization (i.e., efflux, or respiration) of carbon in soil [23,24,37]. We found that the addition of larger detritivores, regardless of warming treatment, altered RH. However, despite similar invertebrate densities at both sites, the effects of millipede and earthworm abundance on RH were apparent only in the low latitude site (Duke Forest) when placed in a common garden. Perhaps the burrowing taxa at these two sites represent different species pools that vary in behaviors related to feeding, burrowing, and redistributing soil organic matter in ways that yield higher RH [37,38].

Although ecosystem models [e.g., 2] generally suggest that soil communities are controlled predominantly by bottom-up forces, a growing body of work highlights the potential of trophic interactions to limit microbial activity [14,19,20,39,40]. When microbes are not limited by temperature, top-down control emerges as an important regulatory force [10]. Multiple studies have shown that warming strengthens the effects of predators on lower trophic levels and nutrient cycling in other systems [21,28,29]. In some cases these invertebrate impacts are equal
to or greater than the direct effects of warming on nutrient cycling [41]. In our study, warming did not alter the composition of macroinvertebrate communities, but the response of burrower mortality to warming varied with food web structure. Macroinvertebrate mortality was more variable, and responsive to warming, when multiple trophic groups were present.

Our work highlights that, although the direct effects of climate change have the potential to influence the functioning of terrestrial ecosystems, the indirect effects—mediated through

![Fig 3. NMDS plot for macroinvertebrate communities extracted from soil cores collected at Harvard Forest (top panel) and Duke Forest (bottom panel) warming chambers.](image)

The colors represent the average air temperature in chambers April 2010-June 2013; the yellow to red color gradient represents cooler to warmer chambers.

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**Table 1.** Model results for Harvard Forest macrofauna common garden mesocosms. Also listed are the range of values observed across treatments.

| Parameter                        | Min-Max     | df  | L   | P    |
|----------------------------------|-------------|-----|-----|------|
| Air temperature in original warming chamber | 9.0–14.0°C  | 11  | 0.006 | 0.94 |
| Soil moisture in original warming chamber | 0.11–0.19 VWC | 11  | 0.074 | 0.78 |
| Coleoptera abundance             | 7–18        | 11  | 0.22 | 0.64 |
| Araneae abundance                | 1–7         | 11  | 0.87 | 0.35 |
| Formicidae abundance             | 1–20        | 11  | 0.001 | 0.97 |
| Diplopoda abundance              | 0–17        | 11  | 0.54 | 0.46 |
| Taxonomic richness               | 4–7         | 11  | 0.36 | 0.55 |

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changes in the biological community—are likely to be more important in governing soil carbon emissions. This finding supports a growing body of work in aboveground ecology, showing that the indirect effects of change in the biological community can overwhelm the initial direct effects of climate change [40,42,43]. However, our work suggests that warming alone is unlikely to drive these changes. It is important to explore the interacting effects of other global change factors (e.g. N addition and land use change) to understand fully the impacts of anthropogenic activity for the functioning of temperate forests.

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Author Contributions

Conceived and designed the experiments: SLP ARC JK TWC. Performed the experiments: SLP ARC JK TWC. Analyzed the data: SLP AM TWC. Wrote the paper: SLP AM ARC JK TWC.

References

1. Schlesinger WH, Andrews JA (2000) Soil respiration and the global carbon cycle. Biogeochemistry 48: 7–20.
2. Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440: 165–173. PMID: 16525463
3. Wieder WR, Bonan GB, Allison SD (2013) Global soil carbon projections are improved by modelling microbial processes. Nature Climate Change 3: 909–912.
4. Bradford MA, Davies CA, Frey SD, Maddox TR, Melillo JM, et al. (2008) Thermal adaptation of soil microbial respiration to elevated temperature. Ecology Letters 11: 1316–1327. doi:10.1111/j.1461-0248.2008.01251.x PMID: 19046360
5. Allison SD, Wallenstein MD, Bradford MA (2010) Soil-carbon response to warming dependent on microbial physiology. Nature Geoscience 3: 336–340.
6. Baveye P, Mysiak J, Laba M (2009) Uncertainties in environmental modelling and consequences for policy making. Dordrecht; London: Springer. 401 p.
7. Bardgett RD, Freeman C, Ostle NJ (2008) Microbial contributions to climate change through carbon cycle feedbacks. Isme Journal 2: 805–814. doi: 10.1038/ismej.2008.58 PMID: 18615117
8. Wall DH (2012) Soil ecology and ecosystem services. Oxford: Oxford University Press. 406 p.
9. Schmitz OJ, Raymond PA, Estes JA, Kurz WA, Holtgrieve GW, et al. (2014) Animating the Carbon Cycle. Ecosystems 17: 344–359.

Table 2. Model results for Duke Forest macrofauna common garden mesocosms.

| Parameter                                | Min-Max               | df | L   | P    |
|------------------------------------------|-----------------------|----|-----|------|
| Air temperature in original warming chamber | 15.0–21.5°C           | 12 | 2.9 | 0.089|
| Soil moisture in original warming chamber   | 0.11–0.28 VWC         | 12 | 2.1 | 0.14 |
| Microbial biomass                         | 204–283 μg C /g       | 12 | 9.5 | 0.002|
| Megadrilacea abundance                    | 0–10                  | 12 | 3.2 | 0.072|
| Formicidae abundance                      | 0–8                   | 12 | 0.91| 0.34 |
| Coleoptera abundance                      | 4–17                  | 12 | 0.15| 0.70 |
| Araneae abundance                         | 0–3                   | 12 | 0.14| 0.71 |
| Diplopoda abundance                       | 0–7                   | 12 | 4.5 | 0.035|
| Taxonomic richness                        | 3–6                   | 12 | 0.17| 0.68 |

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10. Crowther T, Thomas SM, Maynard DS, Baldrian P, Covey K, et al. (2015) Biotic interactions mediate soil microbial feedbacks to climate change. PNAS In Press.
11. Lavelle P, Decaens T, Aubert M, Barot S, Blouin M, et al. (2006) Soil invertebrates and ecosystem services. European Journal of Soil Biology 42: S3–S15.
12. Barrett JE, Virginia RA, Wall DH, Adams BJ (2008) Decline in a dominant invertebrate species contributes to altered carbon cycling in a low-diversity soil ecosystem. Global Change Biology 14: 1734–1744.
13. Setälä H (2005) Does biological complexity relate to functional attributes of soil food webs? In: de Ruiter PC, Wolters V, Moore JC, editors. Dynamic Food Webs: Multispecies Assemblages, Ecosystem Development and Environmental Change. Burlington, MA, U.S.A.: Elsevier, Inc. pp. 308–320.
14. Crowther TW, Boddy L, Jones TH (2011) Outcomes of fungal interactions are determined by soil invertebrate grazers. Ecology Letters 14: 1134–1142. doi:10.1111/j.1461-0248.2011.01682.x PMID: 21929699
15. Bradford MA, Jones TH, Bardgett RD, Black HIJ, Boag B, et al. (2002) Impacts of soil faunal community composition on model grassland ecosystems. Science 298: 615–618. PMID: 12386334
16. Crowther TW, Jones TH, Boddy L, Baldrian P (2011) Invertebrate grazing determines enzyme production by basidiomycete fungi. Soil Biology & Biochemistry 43: 2060–2068.
17. Heemsbergen DA, Berg MP, Loreau M, van Haj JR, Faber JH, et al. (2004) Biodiversity effects on soil processes explained by interspecific functional dissimilarity. Science 306: 1019–1020. PMID: 15528441
18. Wardle DA (2006) The influence of biotic interactions on soil biodiversity. Ecology Letters 9: 870–886. PMID: 16796577
19. Crowther TW, Stanton DWG, Thomas SM, A’Bear AD, Hiscox J, et al. (2013) Top-down control of soil fungal community composition by a globally distributed keystone consumer. Ecology 94: 2518–2528. PMID: 2440503
20. Crowther TW, Jones TH, Boddy L (2011) Species-specific effects of grazing invertebrates on mycelial emergence and growth from woody resources into soil. Fungal Ecology 4: 333–341.
21. Wall DH, Bradford MA, St John MG, Trofymow JA, Behan-Pelletier V, et al. (2008) Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. Global Change Biology 14: 2661–2677.
22. Nielsen UN, Ayres E, Wall DH, Bardgett RD (2011) Soil biodiversity and carbon cycling: a review and synthesis of studies examining diversity-function relationships. European Journal of Soil Science 62: 105–116.
23. Lubbers IM, van Groenigen KJ, Fonte SJ, Six J, Brussaard L, et al. (2013) Greenhouse-gas emissions from soils increased by earthworms. Nature Climate Change 3: 187–194.
24. Kuiper I, de Deyn GB, Thakur MP, van Groenigen JW (2013) Soil invertebrate fauna affect N2O emissions from soil. Global Change Biology 19: 2814–2825. doi: 10.1111/gcb.12232 PMID: 23625707
25. Mikola J, Setälä H (1998) No evidence of trophic cascades in an experimental microbial-based soil food web. Ecology 79: 153–164.
26. Laakso J, Setälä H (1999) Population- and ecosystem-level effects of predation on microbial-feeding nematodes. Oecologia 120: 279–286.
27. Best ML, Welsh JHH (2014) The trophic role of a forest salamander: impacts on invertebrates, leaf litter retention, and the humification process. Ecosphere 5: art16.
28. Barton BT, Beckerman AP, Schmitz OJ (2009) Climate warming strengthens indirect interactions in an old-field food web. Ecology 90: 2346–2351. PMID: 19769112
29. Jochum M, Schneider FD, Crowe TP, Brose U, O’Gorman EJ (2012) Climate-induced changes in bottom-up and top-down processes independently alter a marine ecosystem. Philosophical Transactions of the Royal Society B-Biological Sciences 367: 2962–2970.
30. Prather CM, Pelini SL, Laws A, Rivest E, Wolzt M, et al. (2013) Invertebrates, ecosystem services and climate change. Biological Reviews 88: 327–348. doi: 10.1111/brv.12002 PMID: 23217156
31. Lang B, Rail BC, Brose U (2012) Warming effects on consumption and intraspecific interference competition depend on predator metabolism. Journal of Animal Ecology 81: 516–523. doi: 10.1111/j.1365-2666.2011.01931.x PMID: 22112157
32. Zhao C, Griffin JN, Wu X, Sun S (2013) Predatory beetles facilitate plant growth by driving earthworms to lower soil layers. Journal of Animal Ecology 82: 749–758. doi: 10.1111/j.1365-2666.2012.012058 PMID: 23419174
33. Pelini SL, Bowles FP, Ellison AM, Gotelli NJ, Sanders NJ, et al. (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.
34. Pough FH, Smith EM, Rhodes DH, Collazo A (1987) The Abundance of Salamanders in Forest Stands with Different Histories of Disturbance. Forest Ecology and Management 20: 1–9.

35. Scott-Denton LE, Rosenstiel TN, Monson RK (2006) Differential controls by climate and substrate over the heterotrophic and rhizospheric components of soil respiration. Global Change Biology 12: 205–216.

36. Ellison AM, Gotelli NJ, Sanders NJ, Dunn RR (2009) Ants Under Climate Change at Harvard Forest and Duke Forest since 2009. 10.6073/pasta/be0b964a5caedb39fc89006eba29c9f7: Long Term Ecological Research Network.

37. Crumsey JM, Le Moine JM, Capowiez Y, Goodsitt MM, Larson SC, et al. (2013) Community-specific impacts of exotic earthworm invasions on soil carbon dynamics in a sandy temperate forest. Ecology 94: 2827–2837. PMID:24597228

38. Makoto K, Arai M, Kaneko N (2014) Change the menu? Species-dependent feeding responses of millipedes to climate warming and the consequences for plant-soil nitrogen dynamics. Soil Biology & Biochemistry 72: 19–25.

39. Moore JC, McCann K, Setälä H, De Ruiter PC (2003) Top-down is bottom-up: Does predation in the rhizosphere regulate aboveground dynamics? Ecology 84: 846–857.

40. Post E, Pedersen C (2008) Opposing plant community responses to warming with and without herbivores. Proceedings of the National Academy of Sciences of the United States of America 105: 12353–12358. doi:10.1073/pnas.0802421105 PMID:18719116

41. Rouifed S, Handa IT, David JF, Hättenschwiler S (2010) The importance of biotic factors in predicting global change effects on decomposition of temperate forest leaf litter. Oecologia 163: 247–256. doi:10.1007/s00442-009-1528-1 PMID:20033823

42. Manning P, Newington JE, Robson HR, Saunders M, Eggers T, et al. (2006) Decoupling the direct and indirect effects of nitrogen deposition on ecosystem function. Ecology Letters 9: 1015–1024. PMID:16925650

43. Suttle KB, Thomsen MA, Power ME (2007) Species interactions reverse grassland responses to changing climate. Science 315: 640–642. PMID:17272720