

Reduced feeding activity of soil detritivores under warmer and drier conditions

Madhav P. Thakur^{1,2*}, Peter B. Reich^{3,4}, Sarah E. Hobbie⁵, Artur Stefanski³, Roy Rich³, Karen E. Rice³, William C. Eddy⁶ and Nico Eisenhauer^{1,2}

Anthropogenic warming is projected to trigger positive feedbacks to climate by enhancing carbon losses from the soil¹. While such losses are, in part, due to increased decomposition of organic matter by invertebrate detritivores, it is unknown how detritivore feeding activity will change with warming², especially under drought conditions. Here, using four-year manipulation experiments in two North American boreal forests, we investigate how temperature (ambient, ambient +1.7 °C and ambient +3.4 °C) and rainfall (ambient and -40% of the summer precipitation) perturbations influence detritivore feeding activity. In contrast to general expectations^{1,3}, warming had negligible net effects on detritivore feeding activity at ambient precipitation. However, when combined with precipitation reductions, warming decreased feeding activity by ~14%. Across all plots and dates, detritivore feeding activity was positively associated with bulk soil microbial respiration. These results suggest slower rates of decomposition of soil organic matter and thus reduced positive feedbacks to climate under anthropogenic climate change.

Soil invertebrate detritivores are crucial drivers of the decomposition of soil organic matter^{4,5}, and the decomposition of soil organic matter is key to carbon sequestration in soil^{1,6–8}. Invertebrate detritivores contribute to about 30–40% of decomposition of soil organic matter via their feeding activities on detritus and soil microorganisms^{9,10}. Recent studies have predicted that ongoing climate warming increases soil carbon losses globally by increasing decomposition rates in the soil^{3,11}. However, these predictions rely mostly on enhanced soil microbial activities in response to climate warming¹², without considering the feeding responses of soil invertebrate detritivores (hereafter, ‘soil detritivores’ for brevity) to climate warming.

Ectothermic organisms, such as soil microorganisms and soil detritivores, generally exhibit greater activity with warming because of elevated metabolic demands¹³. However, there are at least two key constraints for higher metabolism of ectotherms at higher temperature that could minimize (or even reverse) greater activity in response to warming¹⁴. First, process rates, such as feeding or respiration at higher temperature, often acclimatize to warmer temperature by returning to rates exhibited at ambient temperature¹⁵. Soil microorganisms occasionally show thermal acclimatization after a given period of time^{16–18}, possibly dependent on the rate of warming¹⁹ and mostly owing to adjustments in their substrate-use efficiency at higher temperature^{14,15}. However, the relationship between substrate-use efficiency of soil microorganisms and soil carbon dynamics remains unclear due to the lack of a general pattern^{20–22}.

Furthermore, our understanding of soil detritivore acclimatization to warming is extremely limited as most of the evidence of their greater activity at higher temperature comes from short-term laboratory incubation studies^{23,24}, which may not be of sufficient duration to allow thermal acclimatization in detritivores. The second constraint involves potential resource limitation for ectothermic organisms in warmed conditions. Warming could reduce the activity of ectothermic detritivore organisms when warming increases resource or substrate depletion in soil^{25–27}, such as warming-induced reduction in soil water. In fact, climate warming seems to increase soil microbial activity only in soils with sufficiently moist conditions^{1,28}. An increasing frequency of summer drought in terrestrial biomes²⁹ thus could also reduce the expected increase of detritivore feeding activity at higher temperatures, as demonstrated for soil microorganisms^{28,30}.

In this study, we report the feeding activity of soil detritivores in response to climate warming using a highly resolved temporal dataset (more than 40 time points) spanning across four years. Furthermore, we investigate the interactive effects of climate warming and summer drought (via reduced summer precipitation) on the feeding activity of soil detritivores. Our results are based on two independent southern boreal forest field experiments with three levels of climate warming (ambient, ambient +1.7 °C and ambient +3.4 °C) crossed with ambient precipitation and reduced summer precipitation. The warming levels were chosen to meet the two target levels of simultaneous plant and soil warming as per the predictions of the climate models for approximately 75–100 years from now^{31,32}. We measured the feeding activity of soil detritivores using a rapid ecosystem assessment technique (bait lamina strips³³) every two weeks in the growing season from 2012 to 2015 (usually from April to November). We hypothesize that climate warming will enhance the feeding activity of soil detritivores, but only at ambient precipitation.

The main effects of experimental warming and reduced precipitation on the feeding activity of soil detritivores were not significant (Table 1). However, warming reduced the feeding activity of soil detritivores under the low precipitation treatment (Fig. 1a,b and Table 1; significant warming × precipitation interaction), especially from the middle (for example, July) through to the late periods (for example, November) of the growing season (Fig. 1a). Overall, the feeding activity was ~14% lower in the +3.4 °C treatment under low precipitation compared to either the +3.4 °C treatment under ambient precipitation or the ambient temperature and ambient precipitation treatment (which were similar) (Fig. 1b).

¹German Centre for Integrative Biodiversity Research Halle–Jena–Leipzig, Leipzig, Germany. ²Institute of Biology, Leipzig University, Leipzig, Germany. ³Department of Forest Resources, University of Minnesota, St. Paul, MN, USA. ⁴Hawkesbury Institute for the Environment, University of Western Sydney, Penrith, New South Wales, Australia. ⁵Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN, USA. ⁶Department of Plant Biology, University of Illinois Urbana–Champaign, Urbana, IL, USA. *e-mail: madhav.prakash.thakur@gmail.com

Table 1 | Results from linear mixed-effects models for treatment effects on soil detritivore feeding activity

Treatments	Soil detritivore feeding activity
Experimental warming (W)	$F_{1,1680} = 1.79$
Reduced precipitation (P)	$F_{1,1680} = 0.28$
W × P	$F_{1,1680} = 10.37^*$
Random effects	
Year	0.29 (0.53)
Day of the year/site	0.21 (0.46)
Day of the year/site/block	<0.001 (<0.001)

The denominator degrees of freedom are based on the Satterthwaite approximation. Variance and standard deviations (in brackets) are given for the random effects used in models (see Methods for details). * $P < 0.01$.

To test whether the treatment effects on detritivore feeding activity can be explained by changes in the microenvironment, we also analysed the results using models that included data on continuously measured soil water content and soil temperature in the plots (also more than 40 time points across four years). Because of seasonal changes in soil temperature and soil water content, we ran generalized additive regression models with soil temperature and soil water as smooth terms. These models also revealed an interactive effect of soil temperature and soil water content on detritivore feeding activity (Table 2), agreeing with our experimental treatment results (Table 1). In general, the feeding activity of soil detritivores was low when soils were cold and wet or warm and dry, and high when soils were warm and wet or cold and dry (Fig. 2).

To compare our results of detritivore feeding activity with other commonly reported ecosystem processes, we further examined the patterns of total soil respiration and bulk soil microbial respiration (with a similar temporal resolution to that of detritivore feeding activity; that is, more than 40 time points across four years) in warmed and reduced precipitation treatments. We found that total soil respiration increased with experimental warming only in the reduced precipitation treatments, whereas it did not change with experimental warming in the ambient precipitation treatments (Supplementary Fig. 1a and Supplementary Table 1). These responses of total soil respiration thus contradicted the observed

decline in detritivore feeding activity in response to warming and reduced precipitation (Fig. 1b).

Bulk soil microbial respiration decreased in the ambient as well as in the warmest temperature treatments under reduced precipitation compared to the ambient warming and ambient precipitation treatments (Supplementary Fig. 1b and Supplementary Table 1). The significant decline in soil microbial respiration in the warmest temperature and reduced precipitation treatments resembled the decline in detritivore feeding activity under the same treatment combination (Fig. 1b). Accordingly, we found a significantly positive correlation between detritivore feeding activity and soil microbial respiration across all treatments and sampling dates (Supplementary Fig. 2).

Climate warming and reduced precipitation are two of the main global change factors determining the effect of soil organisms on the decomposition of soil organic matter. Overall, our results show that climate warming of +3.4 °C, in combination with reduced precipitation, reduced the feeding activity of soil detritivores. This was mainly due to warmer and drier soils, which occurred, as expected, more frequently in this treatment combination. In contrast, warming had only negligible net effects on soil detritivore feeding activity in the ambient precipitation treatment, because warming modestly enhanced activity in cool wet periods (for example, spring), which offset warming-induced lower activity later in the growing season (Fig. 1a and Supplementary Figs. 3 and 4). These results contradict the assumption of greater feeding activity of invertebrates (within their thermal limits) at higher temperature^{24,34}.

Drier habitats imply drier substrates for detritivore species, which are difficult to ingest and digest⁴. As a consequence, mortality among detritivore species could peak in drier soil due to the reduction of both foraging and reproductive success^{35–37}. Furthermore, when warming increases the feeding requirements of ectothermic detritivores^{38,39}, failure to forage in drier soil conditions either enhances their mortality or they disperse to more favourable habitats. We speculate that these two possibilities are plausible scenarios in this study, leading to the reduced feeding activity of soil detritivores in warm and dry soil (Figs. 1b and 2). The lack of an overall warming-induced increase in the net feeding activity over the experimental period (Fig. 1b) was due to shorter durations of peak activities at elevated temperatures across the vegetation growing period (Fig. 1a). Surprisingly, warming treatments were wetter at the start of the growing season (Supplementary Fig. 4), which may have affected the strength of the net effects of

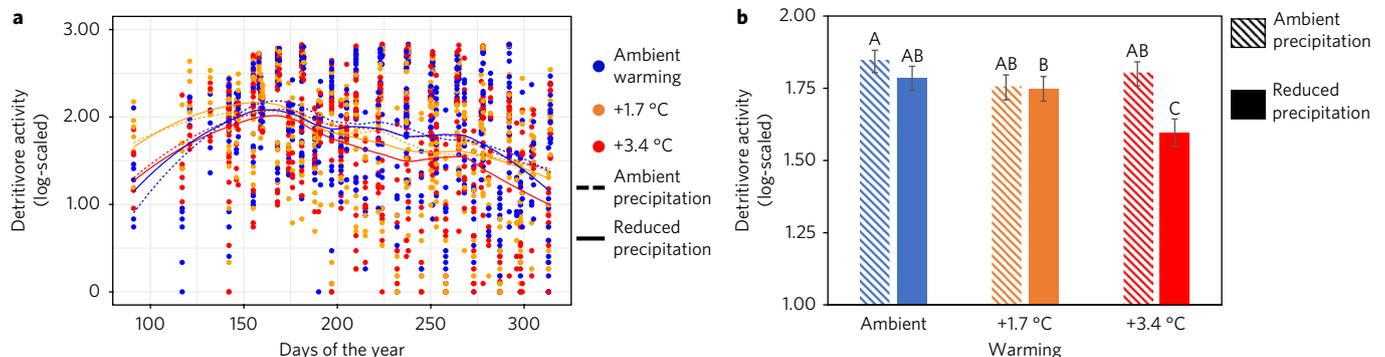


Fig. 1 | Soil detritivore feeding activity in response to experiment warming and reduced precipitation. **a**, Temporal pattern of detritivore feeding activity in response to experimental warming and reduced precipitation. Data shown here are from four years (2012–2015) of detritivore feeding activity measurements at two independent boreal forest sites. The curves are based on ‘loess’ smoothing function with $\lambda = 0.5$ from the ‘ggplot2’ package in R. For each time point, we assessed 18 plots per site (see Methods for details). **b**, Mean (\pm s.e.) detritivore feeding activity in response to warming and precipitation treatments. The bar diagram is based on average detritivore feeding activity (log-scaled) from four years of in situ measurements and two independent sites. The letters on top of the bars are from post-hoc Tukey honest significant difference tests run on mixed-effects models; letters A, B and C indicate significant statistical difference, whereas AB is only significantly different to C. In both panels, blue, orange and red refer to ambient, +1.7 °C and +3.4 °C warming, respectively. The dashed and solid lines and bars refer to ambient and reduced precipitation, respectively.

Table 2 | Results from GAMMs with soil temperature and soil water as smooth terms

Soil abiotics	Soil detritivore feeding activity
Soil temperature	$F_{1,1695.79} = 6.72^*$
Soil water	$F_{4,57,1695.79} = 0.55$
Soil temperature \times soil water	$F_{16,63,1695.79} = 0.86^{**}$
Random effects	
Year	8.46 (2.91)
Site	2.62 (1.62)
Site/block	0.01 (0.13)

Variance and standard deviations (in brackets) are given for the random effects used in the models. * $P < 0.01$; ** $P < 0.001$.

warming on the detritivore feeding activity. This was, however, driven by the year 2015 when the growing season began earlier than the previous years, which caused a slower thawing of snow in the ambient warming plots than in the warmer plots (Supplementary Fig. 5).

Our results contradict several short-term studies, which have shown warming-induced greater feeding activity of soil invertebrates^{23,24,40,41}. We argue that such positive warming effects could be a transient response of soil invertebrates to warming and may disappear as warming-induced reductions in soil water content intensify with time, as has been suggested for the decline in soil respiration with reductions in soil water content in response to warming^{26,42}. Our total respiration results, however, also contradict this assumption as they were still higher in warmed and reduced precipitation treatments (Supplementary Fig. 1a,b). Although these results are based on a relatively long-term warming experiment (seven years of warming and four years of detritivore feeding measurements), we believe that decadal-scale experiments are needed to provide crucial insights to understand the varying patterns of detritivore feeding and soil respiration in response to warming and drought. The general trend of total soil respiration, which includes autotrophic respiration (plant roots) and heterotrophic respiration, showed resemblance to the widely observed greater soil carbon loss at warmer temperatures⁴³; that is, greater respiration rates in response to soil warming. This significant relationship was, surprisingly, observed only in the reduced precipitation treatment. Moreover, the observed mismatch between total soil respiration and detritivore feeding activity at higher temperature indicates complex shifts in the contributions of plants, soil microorganisms and soil detritivores to soil carbon dynamics in warmer boreal forests, potentially due to their varying levels of temperature sensitivities.

Detritivore communities may also acclimatize to warmer climate when sufficient amounts of resources are available¹⁵. Thermal acclimatization might explain the negligible increase in detritivore feeding in the warmed ambient precipitation treatments in our study (Fig. 1b), given that our method of feeding measurements included regularly added substrate (see Methods). Future studies are required to directly assess the potential of thermal acclimatization of soil detritivores. For instance, this could potentially be done by assessing the feeding rates and assimilation efficiencies of soil detritivores from field experiments by exposing them to different temperatures in long-term laboratory trials.

The feeding activity of soil detritivores is a crucial first step in the decomposition of soil organic matter⁴, and their reduced activity in response to joint warming and reduced precipitation can potentially slow down the decomposition of soil organic matter. Lower feeding rates of detritivores can also directly affect the decomposition of organic matter by microbial communities. For instance, the fragmentation of litter would be lower at reduced

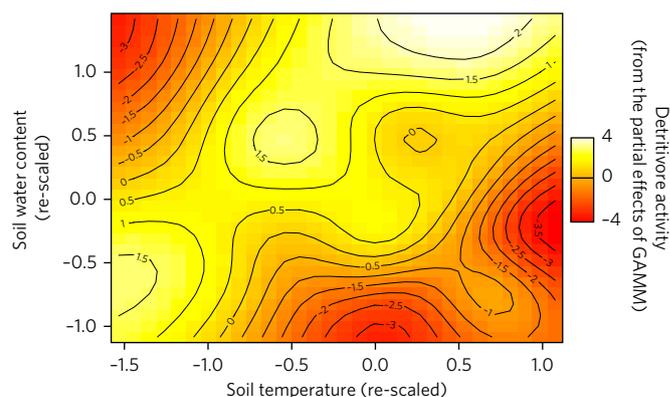


Fig. 2 | Interactive effects of soil temperature and soil water content on the feeding activity of soil detritivores. The heat map is based on the partial residuals of the smooth terms (soil temperature and soil water) used in generalized additive models. Both soil temperature and soil water were re-scaled using the 'arm' package⁴⁶.

feeding activity of detritivores, leading to slower decomposition by microbial communities⁴.

Our results provide novel insights into the climate-dependent dynamics of detritivore feeding activity in boreal forests, which are predicted to get warmer and drier in the future⁴⁴. We recommend that future studies should also investigate warming effects on soil biological activity in winter months (which were not feasible in our study) to improve our understanding of the complex relationships between snow cover dynamics and soil biological processes⁴⁵. Nevertheless, our findings encourage next-generation earth system models to include soil detritivore responses together with plant and soil microbial responses for improving the predictions of soil carbon dynamics under anthropogenic climate change.

Methods

Methods, including statements of data availability and any associated accession codes and references, are available at <https://doi.org/10.1038/s41558-017-0032-6>.

Received: 30 May 2017; Accepted: 20 November 2017;
Published online: 18 December 2017

References

- Davidson, E. A. & Janssens, I. A. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* **440**, 165–173 (2006).
- Bradford, M. A. et al. Managing uncertainty in soil carbon feedbacks to climate change. *Nat. Clim. Change* **6**, 751–758 (2016).
- Crowther, T. et al. Quantifying global soil C losses in response to warming. *Nature* **540**, 104–108 (2016).
- Adl, S. *The Ecology of Soil Decomposition* (CABI Publishing, Trowbridge, 2003).
- Wolters, V. Invertebrate control of soil organic matter stability. *Biol. Fertil. Soils* **31**, 1–19 (2000).
- Prescott, C. E. Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? *Biogeochemistry* **101**, 133–149 (2010).
- Six, J., Conant, R. T., Paul, E. A. & Paustian, K. Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. *Plant Soil* **241**, 155–176 (2002).
- Jastrow, J. D., Amonette, J. E. & Bailey, V. L. Mechanisms controlling soil carbon turnover and their potential application for enhancing carbon sequestration. *Clim. Change* **80**, 5–23 (2007).
- Verhoef, H. & Brussaard, L. Decomposition and nitrogen mineralization in natural and agroecosystems: the contribution of soil animals. *Biogeochemistry* **11**, 175–211 (1990).
- Seastedt, T. The role of microarthropods in decomposition and mineralization processes. *Annu. Rev. Entomol.* **29**, 25–46 (1984).
- Pries, C. E. H., Castanha, C., Porras, R. & Torn, M. S. The whole-soil carbon flux in response to warming. *Science* **355**, 1420–1423 (2017).

12. Allison, S. D., Wallenstein, M. D. & Bradford, M. A. Soil-carbon response to warming dependent on microbial physiology. *Nat. Geosci.* **3**, 336–340 (2010).
13. Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M. & Charnov, E. L. Effects of size and temperature on metabolic rate. *Science* **293**, 2248–2251 (2001).
14. Tucker, C. L., Bell, J., Pendall, E. & Ogle, K. Does declining carbon-use efficiency explain thermal acclimation of soil respiration with warming? *Glob. Change Biol.* **19**, 252–263 (2013).
15. Bradford, M. A. Thermal adaptation of decomposer communities in warming soils. *Front. Microbiol.* **4**, 1–16 (2013).
16. Crowther, T. W. & Bradford, M. A. Thermal acclimation in widespread heterotrophic soil microbes. *Ecol. Lett.* **16**, 469–477 (2013).
17. Melillo, J. M. et al. Soil warming and carbon-cycle feedbacks to the climate system. *Science* **298**, 2173–2176 (2002).
18. Luo, Y., Wan, S., Hui, D. & Wallace, L. L. Acclimatization of soil respiration to warming in a tall grass prairie. *Nature* **413**, 622–625 (2001).
19. Sishi, D., Inglett, P., Gerber, S. & Inglett, K. Rate of warming affects temperature sensitivity of anaerobic peat decomposition and greenhouse gas production. *Glob. Change Biol.* <http://dx.doi.org/10.1111/gcb.13839> (2017).
20. Sinsabaugh, R. L., Manzoni, S., Moorhead, D. L. & Richter, A. Carbon use efficiency of microbial communities: stoichiometry, methodology and modelling. *Ecol. Lett.* **16**, 930–939 (2013).
21. Hagerty, S. B. et al. Accelerated microbial turnover but constant growth efficiency with warming in soil. *Nat. Clim. Change* **4**, 903–906 (2014).
22. Frey, S. D., Lee, J., Melillo, J. M. & Six, J. The temperature response of soil microbial efficiency and its feedback to climate. *Nat. Clim. Change* **3**, 395–398 (2013).
23. Lang, B., Rall, B. C. & Brose, U. Warming effects on consumption and intraspecific interference competition depend on predator metabolism. *J. Anim. Ecol.* **81**, 516–523 (2012).
24. A'Bear, A. D., Boddy, L. & Hefin Jones, T. Impacts of elevated temperature on the growth and functioning of decomposer fungi are influenced by grazing collembola. *Glob. Change Biol.* **18**, 1823–1832 (2012).
25. Eliasson, P. E. et al. The response of heterotrophic CO₂ flux to soil warming. *Glob. Change Biol.* **11**, 167–181 (2005).
26. Conant, R. T. et al. Temperature and soil organic matter decomposition rates—synthesis of current knowledge and a way forward. *Glob. Change Biol.* **17**, 3392–3404 (2011).
27. Kirschbaum, M. Soil respiration under prolonged soil warming: are rate reductions caused by acclimation or substrate loss? *Glob. Change Biol.* **10**, 1870–1877 (2004).
28. Allison, S. D. & Treseder, K. K. Warming and drying suppress microbial activity and carbon cycling in boreal forest soils. *Glob. Change Biol.* **14**, 2898–2909 (2008).
29. IPCC *Climate Change 2014: Synthesis Report* (eds Core Writing Team et al.) (IPCC, 2014).
30. Schindlbacher, A. et al. Soil respiration under climate change: prolonged summer drought offsets soil warming effects. *Glob. Change Biol.* **18**, 2270–2279 (2012).
31. IPCC *Climate Change 2013: The Physical Science Basis* (eds Stocker, T. F. et al.) (Cambridge Univ. Press, 2014).
32. Rich, R. et al. Design and performance of combined infrared canopy and belowground warming in the B4WarmED (Boreal Forest Warming at an Ecotone in Danger) experiment. *Glob. Change Biol.* **21**, 2334–2348 (2015).
33. Von Torne, E. Assessing feeding activities of soil-living animals. I. Bait-lamina-tests. *Pedobiologia* **34**, 89–101 (1990).
34. Rall, B. C. et al. Universal temperature and body-mass scaling of feeding rates. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **367**, 2923–2934 (2012).
35. Lindberg, N., Engtsson, J. B. & Persson, T. Effects of experimental irrigation and drought on the composition and diversity of soil fauna in a coniferous stand. *J. Appl. Ecol.* **39**, 924–936 (2002).
36. Staley, J. T. et al. Effects of summer rainfall manipulations on the abundance and vertical distribution of herbivorous soil macro-invertebrates. *Eur. J. Soil Biol.* **43**, 189–198 (2007).
37. Eisenhauer, N. et al. Warming shifts 'worming': effects of experimental warming on invasive earthworms in northern North America. *Sci. Rep.* **4**, 6890 (2014).
38. Vasseur, D. A. & McCann, K. S. A mechanistic approach for modeling temperature-dependent consumer-resource dynamics. *Am. Nat.* **166**, 184–198 (2005).
39. Brown, J., Gillooly, J., Allen, A. & Savage, V. Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789 (2004).
40. Lang, B., Rall, B. C., Scheu, S. & Brose, U. Effects of environmental warming and drought on size-structured soil food webs. *Oikos* **123**, 1224–1233 (2013).
41. Gongalsky, K. B., Persson, T. & Pokarzhvskii, A. D. Effects of soil temperature and moisture on the feeding activity of soil animals as determined by the bait-lamina test. *Appl. Soil Ecol.* **39**, 84–90 (2008).
42. Davidson, E. A., Trumbore, S. E. & Amundson, R. Soil warming and organic carbon content. *Nature* **408**, 789–790 (2000).
43. Bond-Lamberty, B. & Thomson, A. Temperature-associated increases in the global soil respiration record. *Nature* **464**, 579–582 (2010).
44. Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A. Z. & Schepaschenko, D. G. Boreal forest health and global change. *Science* **349**, 819–822 (2015).
45. Schindlbacher, A., Jandl, R. & Schindlbacher, S. Natural variations in snow cover do not affect the annual soil CO₂ efflux from a mid-elevation temperate forest. *Glob. Change Biol.* **20**, 622–632 (2014).
46. Gelman, A. & Yu-Sung, S. arm: Data Analysis Using Regression and Multilevel/Hierarchical Models. R Package v.1.8-6 (2015).

Acknowledgements

We gratefully acknowledge several interns who spent innumerable hours in the field assessing bait lamina strips. We are thankful to S. Zieger and J. Siebert for providing the images of detritivores and bait lamina strips, respectively. M.P.T. and N.E. acknowledge funding by the Deutsche Forschungsgemeinschaft in the frame of the Emmy Noether research group (Ei 862/2). This project also received support from the European Research Council under the European Union's Horizon 2020 research and innovation programme (grant agreement number 677232). Further support came from the German Centre for Integrative Biodiversity Research Halle–Jena–Leipzig, funded by the German Research Foundation (FZT 118). The B4WarmED project is funded by the US Department of Energy (Grant number DE-FG02-07ER64456) and the College of Food, Agricultural and Natural Resource Sciences at the University of Minnesota.

Author contributions

P.B.R. and S.E.H. conceived the B4WarmED experiment. N.E. conceived the study of soil detritivore feeding activity. A.S., R.R., K.E.R. and W.C.E. collected the data. M.P.T. developed the ideas for this manuscript, analysed the data and wrote the manuscript with substantial input from N.E. and P.B.R. All authors contributed to revisions.

Competing interests

The authors declare no competing financial interests.

Additional information

Supplementary information is available for this paper at <https://doi.org/10.1038/s41558-017-0032-6>.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to M.P.T.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Methods

Site description and experimental design. The experiment is located in the temperate–boreal ecotone region of northern Minnesota in North America at two field stations of the University of Minnesota: the Cloquet Forestry Center at Cloquet (46° 40′ 46″ N, 92° 31′ 12″ W) and the Hubachek Wilderness Research Center at Ely (47° 56′ 46″ N, 91° 45′ 29″ W). These two study sites are ~150 km apart³².

The overall design of the experiment comprises two sites, two habitats (closed and open forest canopy) and three warming treatments (ambient, ambient + 1.7 °C and ambient + 3.4 °C), replicated six times. In 2008, warming treatments were established at both sites using infrared heaters for aboveground heating and belowground cables for belowground heating. Warming treatments were set up in both closed (40–60-year-old mixed aspen, birch and fir) and relatively open (cleared in 2007) canopy conditions³². The plots were circular with a diameter of 3 m. The experiment has a randomized block design (each block consists of six plots) nested within sites. Warming treatments are applied from spring to autumn (usually from April to November) every year from the start of the experiment, and do not run during the winter months (from December to February or March) due to logistical constraints (for example, difficulties in maintaining the desired treatment temperature) and uncertainty related to simulating future winter snow depths.

At the start of the experiment, 11 tree species were planted intermixed with the naturally occurring herbaceous and low shrub species. These tree species belong either to the northern temperate climate or the southern boreal climate⁴⁷. The reduced precipitation treatments were applied at the beginning of the year 2012 only in the open canopy plots during the summer months (from June to September), causing a reduction in summer precipitation by about 40% (Supplementary Fig. 6). The open canopy plots represent a common forest canopy disturbance and we expected summer drought effects to be more pronounced in these plots. Moreover, owing to logistic constraints, reduced precipitation treatments were only established in the open canopy. Thus, to assess the interactions of warming and reduced precipitation, soil detritivore feeding activity was carried out only in the open canopy plots at both experimental sites (Cloquet and Ely).

Soil detritivore feeding activity, soil abiotic, and soil respiration measurements.

Soil detritivores comprise several large groups of invertebrates residing in the soil that feed on dead organic matter that enters the soil, as well as on soil microorganisms. Earthworms, isopods, millipedes, enchytraeids, Collembola, oribatid mites and nematodes are usually considered to be the major soil detritivores⁴ (Supplementary Fig. 7). The feeding activity of soil detritivores was measured by inserting bait lamina strips³³ into the upper 10 cm of the soil. Bait lamina strips are commonly used to rapidly assess the feeding activity of soil detritivores^{41,48–50} (Supplementary Fig. 8) and do not represent microbial activity in the soil⁴¹. Previous studies have reported no loss of the substrates used in bait lamina strips in defaunated soil (but with soil microorganisms)⁴¹, and soil invertebrates have been reported as the main drivers of substrate loss from bait lamina strips⁵¹. Each strip contained 16 holes of 2 mm diameter, which were filled with an artificially prepared organic substrate. The substrate was made of 65% cellulose (micro granular), 15% agar (pulverized), 10% loess and 10% wheat bran (finely ground and sieved) by weight. Loess was obtained from the soil adjacent to the field sites. The substrate paste was prepared by adding water (about 15 ml in 2,050 g of solid substrate) and organic fluorescent dye (10 ml) to increase the accuracy of the method⁴⁸. Six strips filled with the substrate material were inserted in each plot and placed at least 2 cm apart from each other. Strips were removed every two weeks and all 16 holes were thoroughly checked for detritivore feeding activity. Empty holes were scored 1 (indicating high feeding activity), whereas holes filled with substrate were scored 0 (indicating no feeding activity)^{33,48}. Some holes were also partially empty and scored 0.5, which indicates intermediate feeding activity of soil detritivores. Hence, detritivore feeding activity could vary between 0 and 16 per strip, with 0 meaning no feeding activity and 16 indicating maximum feeding activity. The scores from six strips from each plot were averaged for statistical analyses. Feeding activity was measured every two weeks from May to November in 2012, 2013, 2014 and 2015. In 2015, we also measured feeding activity in March and April as the growing season for vegetation started earlier this year; however, this varied between the two sites (Supplementary Fig. 9). In total, 172,800 bait lamina holes were assessed, which resulted in 1,770 data points. Bait lamina assessments were performed only during the growing seasons as soil biological activities peak with vegetation growing periods.

The soil water content and soil temperature were measured at each time point at which detritivore feeding activity was determined. The volumetric soil water content (cm³ H₂O per cm³ soil) was measured using a 30 cm Campbell Scientific CS616 probe inserted at an angle of 45° (ref. ³²). The soil water content was measured at a depth of 20 cm from the soil surface. We compared the measurement of soil water content at a depth of 20 cm with the less frequently measured (three times across three years) soil water content of the top 10 cm of the soil (where the detritivore feeding activities were recorded). We found a significant positive correlation (Pearson's coefficient of correlation = 0.43; Supplementary Fig. 10), justifying the use of soil water content at a depth of 20 cm. Although this correlation was significantly positive, we encourage future studies to measure soil water content at multiple soil depths at regular intervals. Soil temperature (°C) was measured using two sealed thermocouples (type T) installed at a depth of 10 cm

and a distance of about 6.6 cm from the nearest heating cable in the soil³². Other details can be found in ref. ³².

Total soil respiration (bulk soil and root respiration) and bulk soil microbial respiration (excluding root respiration) were measured with three olyvinyl chloride collars (10.2 cm in diameter) installed in every plot. Two of these collars per plot extended about 2 cm into the soil enabling the measurement of total soil respiration. The third collar in every plot was inserted extending 40 cm deeper (~48 cm) into the soil to capture only the bulk soil microbial respiration. The visual inspections from soil cores confirmed a negligible amount of plant roots beyond 40 cm soil depth in our experimental plots. All collars for the measurement of soil respiration were kept free of plant cover. Soil CO₂ flux (either total or microbial respiration) was measured using a LI-6400 infrared gas analyzer with attached soil chambers (LI-COR Biosciences). Soil respiration measurements were carried out every two weeks during the vegetation growing period.

Statistical analyses. Soil detritivore feeding activity comprised 44 time points at Cloquet and 41 time points at Ely over the four years of the measurements. Accordingly, we used a repeated-measures mixed-effects analysis of variance with experimental warming (linear term) and reduced precipitation as two fixed effects and day of the year as the random effect. Furthermore, the experimental blocks and two sites were nested within the day of the year. We also used year as a separate random intercept term. The model structure was: soil detritivore feeding activity ~ warming × precipitation + (1|day of the year/site/experimental block) + (1|year). Site- and year-specific differences in the detritivore feeding activity are graphically shown in Supplementary Figs. 9 and 11, respectively. As the ambient soil temperature and soil water varied in the measurement years in both experimental sites (Supplementary Figs. 5 and 12), we included year as a random intercept in all our models. The 'lme4' package in R was used to run the repeated-measures mixed-effects analysis of variance models⁵² and the lmerTest package⁵³ was used to obtain *F* and *P* values with Satterthwaite approximation for degrees of freedom. The feeding activity of soil detritivores was log-transformed (log(*x* + 1)) to improve the model fit. Mixed-effects models were run using the Gaussian error term with linear model assumptions being met (for example, no correlation between fitted versus residual values). Post-hoc Tukey tests were run with the interaction term using the 'multcomp' package⁵⁴. We ran mixed-effects models to investigate the responses of soil respiration (separately for total soil respiration and bulk soil microbial respiration) with the same model structure as for the responses of detritivore feeding activity to warming and reduced precipitation. The analyses on both respiration data were based on 56 time points in Cloquet, and 49 time points in Ely over the four years of measurements (2012–2015).

To compare the results of treatment effects (warming and reduced precipitation) with soil temperature and soil water measurements in the plots, we used these measurements (with the same temporal resolution) to explain the variance in the feeding activity of soil detritivores. Since both soil temperature and soil water fluctuate nonlinearly within a year (Supplementary Figs. 3 and 4), we used generalized additive mixed-effects models (GAMMs) to test their interactive effects on the feeding activity of soil detritivores. Although GAMMs contain linear predictors as linear mixed-effects models do, they include smooth functions of covariates, allowing flexible specifications of relationships without restricting relationships to be linear, quadratic or cubic⁵⁵. The model structure for the GAMM in our analysis was: soil detritivore feeding activity ~ *s*(soil temperature) × *s*(soil water) + (1|site/experimental block) + (1|year), where '*s*' indicates smooth function for GAMM. Please note that we did not use 'day of the year' as a random effect in our GAMM as both soil temperature and soil water changed with the day of the year (Supplementary Figs. 3 and 4). We ran GAMMs using the 'gamma4' package⁵⁶. The test statistics from GAMMs were obtained from the 'itsadug' package⁵⁷. All statistical analyses were run using the R statistical software⁵⁸.

Data availability. Soil detritivore feeding activity, soil abiotic data and R codes for the statistical analysis are available by direct request to the corresponding author.

References

- Reich, P. B. et al. Geographic range predicts photosynthetic and growth response to warming in co-occurring tree species. *Nat. Clim. Change* **5**, 148–152 (2015).
- Eisenhauer, N. et al. Organic textile dye improves the visual assessment of the bait-lamina test. *Appl. Soil Ecol.* **82**, 78–81 (2014).
- Riutta, T., Clack, H., Crockatt, M. & Slade, E. M. Landscape-scale implications of the edge effect on soil fauna activity in a temperate forest. *Ecosystems* **19**, 534–544 (2016).
- Simpson, J. E., Slade, E., Riutta, T. & Taylor, M. E. Factors affecting soil fauna feeding activity in a fragmented lowland temperate deciduous woodland. *PLoS ONE* **7**, e29616 (2012).
- Birkhofer, K. et al. Soil fauna feeding activity in temperate grassland soils increases with legume and grass species richness. *Soil Biol. Biochem.* **43**, 2200–2207 (2011).
- Bates, D., Maechler, M., Bolker, B. M. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48 (2015).

53. Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. B. lmerTest: Tests in Linear Mixed Effects Models. R Package v.2.0-33 (2016).
54. Hothorn, T., Bretz, F. & Westfall, P. Simultaneous inference in general parametric models. *Biom. J.* **50**, 346–363 (2008).
55. Wood, S. N. *Generalized Additive Models: an Introduction with R* (Chapman and Hall, Boca Raton, USA, CRC, 2006).
56. Wood, S. & Scheipl, F. gamm4: Generalized Additive Mixed Models Using 'mgcv' and 'lme4'. R Package v.0.2-3 (2014).
57. Van Rij, J. & Wieling, M. itsadug: Interpreting Time Series and Autocorrelated Data Using GAMMs. R Package v.2.2 (2016).
58. R Development Core Team *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2014).