Warming effects on soil microbial community composition and activity is context-dependent on soil, ecosystem, and experimental factors: A meta-analysis

**ABSTRACT**

Soil temperature affects the abundance and activity of microbes in the soil. Several soil warming experiments conducted over the past decade have reported change in soil microbial abundance and their functional role in the soil. However, the observed changes were not consistent across the studies.  We performed a meta-analysis with a dataset compiled from 62 published warming studies to examine how soil physicochemical characteristics, climate, ecosystem type, and experimental factors impact warming effects on soil microbial community composition and activity. We found that warming effects on total biomass, bacteria, gram-negative bacteria, fungi, and phenoloxidase (PHO) activity were negatively correlated to warming magnitude. However, soil respiration was positively correlated to the magnitude of soil warming. Warming decreased fungal abundance in the agricultural ecosystem, while fungal biomass increased in the old-field ecosystem. In grassland, microbes were insensitive to warming. Higher total biomass, soil respiration, and PHO activity were observed in the alkaline pH range. The infrared heating method increased total biomass and β-1,4-N acetyl-glucosaminidase (NAG) activity, whereas it decreased fungal biomass and PHO activity. The open top chamber (OTC) method showed a positive warming effect on soil fungi. The sensitivity of soil microorganisms to increased soil temperature varied with warming magnitude, warming method, soil pH, and ecosystem type. Microorganisms in disturbed soil appeared to be more sensitive to warming as compared to undisturbed soil. Extreme soil pH also increased microbial sensitivity to temperature.

**Keywords**: soil warming, soil microorganisms, microbial community composition, microbial activity, soil respiration, enzyme activity

**1. Introduction**

The temperature of the earth’s atmosphere has been rising over the past few years. The unprecedented increase in atmospheric temperature alters the structure and functions of the terrestrial ecosystem (Rosenzweig et al., 2007), and these changes drive imbalance to ecosystem carbon budgeting, which can affect C cycle- climate feedback, both positively and negatively (Carey et al., 2016; Zhao et al., 2017).

The soil micro-organisms play a primary role in determining the terrestrial carbon cycle and climate change feedback by carrying out soil organic matter (SOM) decomposition and nutrients cycling in the soil. Soil microbes are highly sensitive to environmental change, such as a change in soil temperature. Therefore, warming-induced changes in soil thermal regime may cause a shift in community composition, diversity, and ecosystem functions of the soil microbes (Johnston et al., 2019). Besides, warming enhances the soil microbes' metabolism, so they become more active and speed up organic matter decomposition, resulting in the greater release of carbon dioxide (CO2) gas from the soil (Lloyd and Taylor, 1994). The effects usually intensify when more than one environmental driver comes into play. For example, warming, coupled with decreased precipitation, was reported to profoundly impact soil microbes' diversity, soil respiration, and overall soil microbial functions than warming alone (Oliveira et al., 2020). Therefore, to fully understand climate change’s impact on ecosystem processes, it is necessary to understand how soil microbial communities behave under changing soil environments.

Soil microbes are usually adapted to prevalent temperature conditions. When the temperature changes, there will be a shift in the microbial community (Rinnan et al., 2009). However, the community composition of soil microbes does not seem to follow a predictable pattern of change. Several warming experiments conducted over different time and locations observed that soil microbes showed variable responses to warming, which was usually dependent on the degree and duration of warming, climatic variables, and soil characteristics. Zhang et al. (2005) reported that total microbial biomass and fungal biomass decreased with the increased soil temperature. However, the total bacterial biomass was not significantly affected. In contrast, Zhang et al. (2014) and Sheik et al. (2011) found higher total microbial biomass in heated plots than in control plots. Similarly, Deangelis et al. (2015) found a 5-degree increase in soil temperature marginally reduced fungal biomass in temperate forest soil, whereas Clemmensen et al. (2013) showed that higher soil temperature in boreal forest stimulates the fungal biomass and activity. Carrillo et al. (2018), during their warming experiment in the mixed-grass prairie, found warming increased the relative abundance of fungi and bacteria while decreased the relative abundance of actinomycetes. On the contrary, Fujimura et al. (2008), from 5 years of warming experiment in the tundra ecosystem, reported no significant change in composition, diversity, and evenness of soil fungi.

An increase in soil temperature usually stimulates soil respiration by increasing CO2 release through autotrophic respiration or accelerating the soil organic matter decomposition (Bond-Lamberty and Thomson, 2010). Soil temperature also regulates the catalysis, production, and degradation rates of the soil extracellular enzymes under field conditions, which have a significant role in determining net CO2 flux in or from the soil (Wallenstein et al., 2010). However, the climatic variables, such as average annual temperature, amount of precipitation received, may influence the soil respiration response to warming, thereby creating inconsistent variation in soil respiration across all biomes (Exbrayat et al., 2013). Temperature dependency on microbial respiration is also influenced by soil physicochemical characteristics such as soil moisture, soil nutrients, and carbon biomass in soil (Davisson and Janssens, 2006). Due to the inconsistent results of warming effects on soil micro-organisms from previous studies, the actual effects of elevated temperature on microbial community composition and activity are not fully understood. We also lack an understanding of how various environmental, climatic and soil characteristics influences the effects of warming on community composition and metabolic activity of soil micro-organisms.

We designed this study to (i) understand how soil microbial abundances and activity changes with warming, concerning both magnitude and duration of warming; and (ii) investigate the role of climate, ecosystems, and soil physicochemical characteristics in determining those changes. Using a meta-analytic approach, we studied the effects of soil warming on soil microbial community composition, soil respiration, and exocellular enzyme activity. We compiled the data (mean and standard deviation) from 42 previously published warming experiments and interpreted the effect size associated with each response variable using a bootstrapping procedure.

**2. Materials and Methods**

**2.1 Literature search**

We conducted an extensive literature survey looking for published papers reporting effects of warming on soil microbial community structure and activity, using Web of Science, and Google Scholar. We performed separate literature searches using a combination of the following keywords: "experimental warming," "elevated temperature," "soil microbial diversity," "soil microbial community structure," "soil microorganisms," "soil fungi," "soil bacteria," "soil respiration," "heterotrophic respiration," "microbial respiration," "soil extracellular enzyme activities," "soil microbial activity." We only included original research articles published between 1995 to 2020.

We established a set of paper selection criteria for our study, which were: (a) studies had reported control data (mean, sample size, and standard deviation (SD) or standard error (SE) alongside treatment data; (b) warming experiment lasted for at least one growing season in the field; we excluded greenhouse studies and other controlled environment experiments) (c) clearly stated warming procedures (e.g., warming technique, the magnitude of warming, and warming duration; (d) climatic conditions, vegetation, land use, soil physicochemical characteristics were similar between control and treatment plots (e) studies that included interacting factors other than temperature had to be designed in the split-plot design with a separate subplot for temperature treatment and (f) we only included studies from relatively dry environments (MAP < 1000 mm).

**2.2 Data extraction**

Based on our pre-established selection criteria, in total, we shortlisted 42 published warming studies for our meta-analysis. (Supplemental Table S1, Fig 1). To assess the microbial community composition, we extracted data related to total microbial biomass, fungal biomass, bacterial biomass, and microbial biomass carbon. Similarly, we also collected data of total soil respiration, microbial respiration, and activity of extracellular soil enzymes activity. The enzymes were categorized into 3 major groups for analysis purpose: C-hydrolyzing enzymes (β-1,4 glucosidase (BG), α-1,4 glucosidase (AG), β-D Cellobiohydrolase (CBH), β-1,4 xylosidase (BX)), N-hydrolyzing enzymes (β-1,4-N acetyl glucosaminidase (NAG), leucine aminopeptidase (LAP)) and Oxidases (Phenol Oxidase (PHO), and Peroxidase (PO). We extracted mean values, standard deviation (SD), and sample size (N) of both control and warmed treatment, from each study, for all the variables we included in our meta-analysis directly from tables, graphs, and published supplementary materials. To extract data from graphical figures, we used WebPlotDigitilizer (<https://apps.automeris.io/wpd/>). We used 10% of the mean as the SD when SD was missing in the paper. If only SE were provided in the paper, we calculated SD as:

SD = SE ×

Additionally, we recorded geographic coordinates, mean annual temperature (MAT), and mean annual precipitation (MAP) of the experiment site, ecosystem type, soil pH, warming methods, warming magnitude or duration, and plant type for each study. If specific data such as MAT, MAP, soil pH were not presented in the paper, we collected such information from other experiments conducted simultaneously at the same site or obtained from the global climate and weather database using geographic coordinates.

**2.3 Data preparation and analysis**

We used log response ratio (lnR), a natural log of the ratio between the arithmetic means of the warming (Xt) and the control treatment (Xc) as effect size (Hedges et al., 1999):

Similarly, we calculated variance (v) of effect size using the following formula:

SDt and SDc are the standard deviations, and Nt and Nc are the sample sizes of warming and control treatments, respectively. We calculated the relative weight (w) as an inverse of variance (v) and the weight was adjusted by dividing the number of observations per study.

The mean effect size and 95% confidence interval (CI) were calculated using a bootstrapping procedure, and the statistical significance was interpreted using 95% CI. The control and treatment were considered statistically significant if the 95% CIs didn’t overlap the zero.

We transformed the mean effect size of each variable to the percentage change as:

**Figures:**

**Map

Description automatically generated**

**Fig. 1.** Map showing the geographical distribution and ecosystem type of 42 warming experiments included in the meta-analysis.

**Chart, box and whisker chart

Description automatically generatedChart, box and whisker chart

Description automatically generated**

**Fig. 2.** Warming effect on soil microbial (a) community structure and (b) metabolic activity. The data shown are mean effect sizes. The error bars represent 95% confidence interval. The numbers indicate the sample size. G- Bacteria: Gram-negative bacteria, G+ bacteria: Gram-positive bacteria, MBC: Microbial biomass carbon, BG: β-1,4 glucosidase, BX: β-1,4 xylosidase, CBH: β- D- cellobiohydrolase, NAG: β-1,4 -N- acetyl glucosaminidase, LAP: Leucine aminopeptidase, PHO: Phenol oxidase, PO: Peroxidase.

Chart, box and whisker chart

Description automatically generated

**Fig. 3.** Warming effects on soil microbial community structure in a) agricultural ecosystem, b) controlled environment, c) grassland ecosystem, and d) old-field ecosystem. Old-field and grassland harbored a greater number of microbes as compared to the agricultural ecosystem. The data shown are mean effect sizes. The error bars represent 95% confidence interval. The numbers indicate the sample size. G- Bacteria: Gram-negative bacteria, G+ bacteria: Gram-positive bacteria, MBC: Microbial biomass carbon.

Chart, diagram, box and whisker chart

Description automatically generated

**Fig. 4.** Warming effects on soil microbial community structure in a) acidic, b) alkaline, and c) neutral soil pH. The data shown are mean effect sizes. The error bars represent 95% confidence interval. The numbers indicate the sample size. G- Bacteria: Gram-negative bacteria, G+ Bacteria: Gram-positive bacteria, MBC: Microbial biomass carbon.

Chart, diagram, box and whisker chart

Description automatically generated

**Fig. 5.** Warming effects on soil microbial community structure when the soil was warmed using a) heating cables, b) infrared heaters, and c) open-top chambers. The data shown are mean effect sizes. The error bars represent 95% confidence interval. The numbers indicate the sample size. G- Bacteria: Gram-negative bacteria, G+ bacteria: Gram-positive bacteria, MBC: Microbial biomass carbon.

Chart, box and whisker chart

Description automatically generated

**Fig. 6.** Warming effects on soil microbial activity in a) acidic, b) alkaline, and c) neutral soil pH. The data shown are mean effect sizes. The error bars represent 95% confidence interval. The numbers indicate the sample size. BG: β-1,4 glucosidase, BX: β-1,4 xylosidase, CBH: β- D- cellobiohydrolase, NAG: β-1,4 -N- acetyl glucosaminidase, LAP: Leucine aminopeptidase, PHO: Phenol oxidase, PO: Peroxidase.

Chart, diagram

Description automatically generated

**Fig. 7.** Warming effects on soil microbial activity when the soil was warmed using a) heating cables, b) infrared heaters, and c) open-top chambers. The data shown are mean effect sizes. The error bars represent 95% confidence interval. The numbers indicate the sample size. BG: β-1,4 glucosidase, BX: β-1,4 xylosidase, CBH: β- D- cellobiohydrolase, NAG: β-1,4 -N- acetyl glucosaminidase, LAP: Leucine aminopeptidase, PHO: Phenol oxidase, PO: Peroxidase.

**3. Results**

**3.1 Predictors of soil microbial community composition and activity under soil warming**

Using the cforest and varimp function in a party package of R, we ranked the predictors based on their predictive performance to determine warming effects on soil microbes. The warming magnitude, warming methods, soil pH, warming duration, ecosystem, and mean annual precipitation (MAP) were the top six predictors; however, irrigation, fertilization, and mean annual temperature (MAT) seem to have little to no influence to determine warming effects on the soil microbial abundance and activity (Supplemental figure S2). The warming magnitude was the most important predictor of warming effects on soil microbes, which revealed that the greater the change in soil temperature is usually associated with the greater difference in microbial abundance and their activity in the soil.

**3.2 Soil microbial community composition**

To evaluate how those predictor variables influenced the effects of warming on soil microbial abundance, we constructed the mixed effect model using the top six predictors as fixed effects and studyID as a random effect. Warming overall increased total biomass by 9.12 %, bacteria by 2.6%, G+ bacteria by 5. 38%, G- bacteria by 3.83%, MBC by 1 %, decreased fungi by 1.44% (Fig. 2a). However, the warming effect was not statistically significant in all microbial groups (Supplemental table S3).

Warming effect on total biomass (z = -2.86, p = 0.0042), bacteria (z = -2.06, p = 0.039), fungi (z = -4.82, p < 0.001), and G- bacteria (z = -2.19, p = 0.0282) was negatively correlated to warming magnitude, but warming effect on MBC and G+ bacteria was not significantly correlated to magnitude of warming. Warming duration and MAP did not seem to have strong influence on either of these microbial groups (Supplemental table S3).

Warming effect on soil fungi was significantly different in grassland (z = 3.306, p = 0.0009) and old field ecosystem (z = 2.834, p = 0.0045) as compared to agricultural ecosystem. In the agricultural ecosystem, warming decreased soil fungi by 17.83 %, whereas it increased fungal biomass in the old field by 39.03% (Fig. 3). In grassland, warming did not alter soil fungal abundance. MBC, total PLFA, bacteria, G+ bacteria, and G- bacteria were not affected by the ecosystem under elevated soil temperature.

Similarly, the warming effects on total microbial biomass increased in alkaline (z = 2.17, p = 0.029) and neutral (z = 2.58, p = 0.0098) pH range relative to acidic pH. Warming increased total biomass in alkaline and neutral soil pH by 14.93% and 7.53%, respectively (Fig. 4). Soil warming methods also influenced the warming effect on soil fungi. Infrared heaters (z =-2.318, p = 0.0204) significantly decreased fungal biomass by 4.98% and increased total biomass by 8.11 %, whereas open top chamber (z = -2.309, p = 0.209) increased fungi by 8.67% (Fig. 5).

**3.3 Soil microbial activity**

Soil warming had a significant effect on the activity of BX (z = -2.12, p = 0.034) and PHO (z = 2.51, p = 0.012); however, warming effects on total soil respiration, microbial respiration, and activity of extracellular soil enzyme (CBH, NAG, BG, LAP and PO) was not statistically significant (Supplemental Table S4). Though the effect was not significant, soil warming increased the total soil respiration and microbial respiration (Fig.2b).

The warming effect on soil respiration (z = 3.82, p = 0.0001) was positively correlated to warming magnitude, and PHO activity was negatively correlated to warming magnitude. Warming magnitude did not alter the warming effect on microbial respiration and other soil enzymes. Similarly, Warming duration only influenced the warming effect on microbial respiration (z = 2.165, p = 0.0304), and MAP did not affect the microbial activity under warming (Supplemental Table S4).

Ecosystem did not change the warming effect on soil microbial activity. The warming effect on soil respiration was significantly lower in neutral pH (z = 2.41, p = 0.015) relative to acidic and alkaline pH. Similarly, the activity of the PHO enzyme under warming was significantly higher in alkaline pH (z = 3.396, p = 0.007) compared to acidic pH and neutral pH (Fig. 6). Soil respiration was not affected by the warming methods, but soil heating with heating cables (z =2.13, p = 0.033) increased BG activity by 5.54%. Infrared heaters increased NAG activity (z = 2.06, p = 0.0394) by 3.12% and decreased PHO activity (z = -2.32, p = 0.0060) by 3.53% (Fig. 7).

4. **Discussion**

Our objective was to evaluate the warming effect on soil microbial community composition and activity and determine different factors influencing the warming effect. We observed that different groups of microbes (i.e., bacteria, fungi, etc.) tended to respond differently to the increased soil temperature and that microbial responses to warming are determined by the magnitude and method of warming, ecosystem type, and soil pH. Warming effects on total microbial biomass, fungi, and bacteria were inversely related to warming magnitude. However, the duration of warming did not affect microbial community composition. Soil fungal abundance was less affected by warming in the old-field and grassland ecosystem than the agricultural ecosystem under warming. Our results also suggest that soil microbes can thrive well in neutral to alkaline pH but cannot tolerate acidic conditions under warming.

Similarly, soil warming positively influenced both total soil respiration and microbial respiration, but most of the enzyme’s activity was negatively correlated to warming (Fig 2b). The warming effect on soil respiration and PHO activity was positively and negatively influenced by warming, respectively. We also observed greater soil respiration and PHO activity in alkaline pH under soil warming. Among the experimental warming methods reported in our study, the infrared heater method showed a stronger influence on soil microbial abundance and activity.

Our analysis showed that as the magnitude of soil warming increased, the total microbial biomass, fungal biomass, and bacterial biomass decreased. Deangelis et al. (2015) also reported that a 5-degree increase in temperature significantly reduced the microbial biomass. Higher warming magnitude increased soil respiration, but it did not affect the warming effect on soil enzymes except PHO. PHO activity decreased with increased warming magnitude. ﻿Suseela et al. (2012) also found that during the non-growing season, medium (2.3 oC) and high (3.2 oC) warming increased soil microbial respiration by 16% and 37%, respectively, compared to the un-warmed treatment. Similar results were was also observed by Nie et al. (2013). In contrast to our finding, (Sistla and Schimel, 2013) reported that the ﻿average hydrolytic enzyme activities in the surface organic soil reduced relative to ambient temperature where oxidative enzyme activity remain unaffected.

We observed microbes were less sensitive to warming in grassland as compared to the agricultural ecosystem. The warming effect in agricultural soil is more detrimental to soil microbes as compared to grassland soil. Zhang et al., (2011) found no significant change in microbial structure in semi-arid grassland, while Bamminger et al. (2016) reported decreased fungal and bacterial abundance in the wheat field. The greater amount of organic matter deposition through litter incorporation in the grassland creates a suitable microhabitat for soil microbes as it enriches the soil with organic carbon (Mukumbuta and Hatano, 2020), which might be the reason why microbes are less affected by warming grassland ecosystems.

In our study, soil microbial abundance was relatively less affected by warming in neutral soil pH than acidic and alkaline pH. Soil respiration, however, was positively influenced by warming in acidic and alkaline pH. A study by Rousk et al., (2009) also reported a greater abundance of soil bacteria and fungi in neutral soil relative to acidic soil. However, they observed no strong influence of pH on soil respiration, though pH influenced microbial growth rate and biomass.

In summary, this meta-analysis showed that warming effects on microbial communities greatly vary depending on the experimental factors, ecosystem, and soil characteristics. Specifically, the higher degree of warming decreased microbial biomass and increased the amount of carbon dioxide released from the soil. Soil warming had a strong effect on soil microbes in cultivated ecosystems as compared to undisturbed grassland. As soil microbes have a crucial role in carbon mineralization and release of CO2 in the atmosphere, it is essential to include microorganisms while constructing climate models. In our study, we summarized the effects of a factor of climate change on microbes in different climatic and environmental conditions. Inclusion of forest ecosystem in the meta-analysis could have produced different results as soil fungal abundance and activity are usually favored by moist, acidic, and C-rich forest soils. Also, we considered one factor of climate change (i.e., warming). Therefore, further exploration is needed regarding microbial response to various climate change factors to make a precise climate change prediction.

Conclusion

**References:**

Bamminger, C., Poll, C., Sixt, C., Högy, P., Wüst, D., Kandeler, E., Marhan, S., 2016. Short-term response of soil microorganisms to biochar addition in a temperate agroecosystem under soil warming. Agriculture, Ecosystems & Environment 233, 308–317. https://doi.org/10.1016/j.agee.2016.09.016

Bond-Lamberty, B., Thomson, A., 2010. Temperature-associated increases in the global soil respiration record. Nature 464, 579–582. https://doi.org/10.1038/nature08930

Carey, J.C., Tang, J., Templer, P.H., Kroeger, K.D., Crowther, T.W., Burton, A.J., Dukes, J.S., Emmett, B., Frey, S.D., Heskel, M.A., Jiang, L., Machmuller, M.B., Mohan, J., Marie, A., Reich, P.B., Reinsch, S., Wang, X., Allison, S.D., Bamminger, C., Bridgham, S., Collins, S.L., Dato, G. de, Eddy, W.C., Enquist, B.J., Estiarte, M., Harte, J., Henderson, A., Johnson, B.R., Steenberg, K., Luo, Y., Marhan, S., Melillo, J.M., Peñuelas, J., Pfeifer-meister, L., Poll, C., Rastetter, E., Tietema, A., 2016. Temperature response of soil respiration largely unaltered with experimental warming 113, 13797–13802. https://doi.org/10.1073/pnas.1605365113

Carrillo, Y., Dijkstra, F., Lecain, D., Blumenthal, D., Pendall, E., 2018. Elevated CO2 and warming cause interactive effects on soil carbon and shifts in carbon use by bacteria. Ecology Letters 21, 1639–1648. https://doi.org/10.1111/ele.13140

Clemmensen, K.E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R.D., Wardle, D.A., Lindahl, B.D., 2013. Roots and Associated Fungi Drive Long-Term Carbon Sequestration in Boreal Forest. Science New Series 339, 1615–1618. https://doi.org/10.1126/science.l232728

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173. https://doi.org/10.1038/nature04514

Deangelis, K.M., Pold, G., Topã§Uoäÿlu, B.D., van Diepen, L.T.A., Varney, R.M., Blanchard, J.L., Melillo, J., Frey, S.D., 2015. Long-term forest soil warming alters microbial communities in temperate forest soils. Frontiers in Microbiology 6. https://doi.org/10.3389/fmicb.2015.00104

Exbrayat, J.F., Pitman, A.J., Zhang, Q., Abramowitz, G., Wang, Y.P., 2013. Examining soil carbon uncertainty in a global model: Response of microbial decomposition to temperature, moisture and nutrient limitation. Biogeosciences 10, 7095–7108. https://doi.org/10.5194/bg-10-7095-2013

Fujimura, K.E., Egger, K.N., Henry, G.H.R., 2008. The effect of experimental warming on the root-associated fungal community of Salix arctica. The ISME Journal 2, 105–114. https://doi.org/10.1038/ismej.2007.89

Johnston, E.R., Hatt, J.K., He, Z., Wu, L., Guo, X., Luo, Y., Schuur, E.A.G., Tiedje, J.M., Zhou, J., Konstantinidis, K.T., 2019. Responses of tundra soil microbial communities to half a decade of experimental warming at two critical depths. Proceedings of the National Academy of Sciences 116, 15096–15105. https://doi.org/10.1073/pnas.1901307116

Lloyd J., Taylor, J.A., 1994. On the Temperature Dependence of Soil Respiration. Functional ecology 8, 315–323.

Mukumbuta, I., Hatano, R., 2020. Do tillage and conversion of grassland to cropland always deplete soil organic carbon? Soil Science and Plant Nutrition 66, 76–83. https://doi.org/10.1080/00380768.2019.1676135

Nie, M., Pendall, E., Bell, C., Gasch, C.K., Raut, S., Tamang, S., Wallenstein, M.D., 2013. Positive climate feedbacks of soil microbial communities in a semi-arid grassland. Ecology Letters 16, 234–241. https://doi.org/10.1111/ele.12034

Oliveira, T.B., Lucas, R.C., Scarcella, A.S.D.A., Contato, A.G., Pasin, T.M., Martinez, C.A., Polizeli, M.D.L.T.D.M., 2020. Fungal communities differentially respond to warming and drought in tropical grassland soil. Molecular Ecology 29, 1550–1559. https://doi.org/10.1111/mec.15423

Rinnan, R., Rousk, J., Yergeau, E., Kowalchuk, G.A., Bã…Ã…Th, E., 2009. Temperature adaptation of soil bacterial communities along an Antarctic climate gradient: predicting responses to climate warming. Global Change Biology 15, 2615–2625. https://doi.org/10.1111/j.1365-2486.2009.01959.x

Rosenzweig, C., Casassa, G., Karoly, D.J., Imeson, a., Liu, C., Menzel, a., Rawlins, S., Root, T.L., Seguin, B., Tryjanowski, P., 2007. Assessment of observed changes and responses in natural and managed systems. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. 79–131. https://doi.org/Milandre climat

Rousk, J., Brookes, P.C., Bååth, E., 2009. Contrasting soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization. Applied and Environmental Microbiology 75, 1589–1596. https://doi.org/10.1128/AEM.02775-08

Sistla, S.A., Schimel, J.P., 2013. Soil Biology & Biochemistry Seasonal patterns of microbial extracellular enzyme activities in an arctic tundra soil : Identifying direct and indirect effects of long-term summer warming. Soil Biology and Biochemistry 66, 119–129. https://doi.org/10.1016/j.soilbio.2013.07.003

Suseela, V., Conant, R.T., Wallenstein, M.D., Dukes, J.S., 2012. Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. Global Change Biology 18, 336–348. https://doi.org/10.1111/j.1365-2486.2011.02516.x

Wallenstein, M., Allison, S.D., Ernakovich, J., Steinweg, J.M., Sinsabaugh, R., 2010. Controls on the Temperature Sensitivity of Soil Enzymes: A Key Driver of In Situ Enzyme Activity Rates, in: Soil Enzymology. Springer Berlin Heidelberg, pp. 245–258. https://doi.org/10.1007/978-3-642-14225-3\_13

Zhang, B., Chen, S., He, X., Liu, W., Zhao, Q., Zhao, L., Tian, C., 2014. Responses of soil microbial communities to experimental warming in alpine grasslands on the Qinghai-Tibet Plateau. PLoS ONE 9. https://doi.org/10.1371/journal.pone.0103859

Zhang, N., Xia, J., Yu, X., Ma, K., Wan, S., 2011. Soil microbial community changes and their linkages with ecosystem carbon exchange under asymmetrically diurnal warming. Soil Biology and Biochemistry. https://doi.org/10.1016/j.soilbio.2011.06.001

Zhang, W., Parker, K.M., Luo, Y., Wan, S., Wallace, L.L., Hu, S., 2005. Soil microbial responses to experimental warming and clipping in a tallgrass prairie. Global Change Biology 11, 266–277. https://doi.org/10.1111/j.1365-2486.2005.00902.x

Zhao, F., Ren, C., Shelton, S., Wang, Z., Pang, G., Chen, J., Wang, J., 2017. Grazing intensity influence soil microbial communities and their implications for soil respiration. Agriculture, Ecosystems & Environment 249, 50–56. https://doi.org/10.1016/j.agee.2017.08.007