Site-specific responses of fungal and bacterial abundances to experimental warming in litter and soil across arctic and alpine tundra

Mathilde Jeanbille[1]*, Karina Clemmensen[1], Jaanis Juhanson[1], Anders Michelsen[2], Elisabeth J. Cooper[3], Greg H.R. Henry[4], Annika Hofgaard[5], Robert D. Hollister[6], Ingibjörg S. Jónsdóttir[7], Kari Klanderud[8], Anne Tolvanen[9], Sara Hallin[1]

[1]Swedish University of Agricultural Sciences, Department of Forest Mycology and Plant Pathology, Uppsala, Sweden; [2]University of Copenhagen, Department of Biology, Terrestrial Ecology Section, Copenhagen, Denmark; [3] UiT - The Arctic University of Norway, Faculty of Biosciences, Fisheries and Economics, Department of Arctic and Marine Biology, Tromsø, Norway; [4]The University of British Columbia, Department of Geography, Vancouver, Canada; [5]Norwegian Institute for Nature Research, Trondheim, Norway; [6]Grand Valley State University, Allendale MI, USA; [7]University of Iceland, Reykjavik, Iceland; [8]Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Norway; [9]Natural Resources Institute Finland (Luke), Oulu, Finland

*Corresponding author: mathilde.jeanbille@gmail.com

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ABSTRACT

Vegetation change of the Arctic tundra due to global warming is a well-known process, but the implication for the belowground microbial communities, key in nutrient cycling and decomposition, is poorly understood. We characterized the fungal and bacterial abundances in litter and soil layers across 16 warming experimental sites at 12 circumpolar locations. We investigated the relationship between microbial abundances and nitrogen (N) and carbon (C) isotopic signatures, indicating shifts in microbial processes with warming. Microbial abundances were 2-3 orders of magnitudes larger in litter than in soil. Local, site-dependent responses of microbial abundances were variable, and no general effect of warming was detected. The only generalizable trend across sites was a dependence between the warming response-ratios and C:N ratio in controls, highlighting a legacy of the vegetation on the microbial response to warming. We detected a positive effect of warming on the litter mass and $\delta^{15}N$, which was linked to bacterial abundance under warmed conditions. This effect was stronger in experimental sites dominated by deciduous shrubs, suggesting an altered bacterial N-cycling with increased temperatures, mediated by the vegetation, and with possible consequences on ecosystem feedbacks to climate change.

Keywords: Tundra, warming, litter, soil, microbial abundance, stable isotopes

INTRODUCTION

Global warming is twice as fast in the Arctic as in other regions on Earth (Meredith et al. 2019), causing profound changes of tundra ecosystems. Vegetation is changing with shrubs and graminoids expanding and growing faster in response to warming, while lichens and mosses are decreasing (Myers-Smith et al. 2011; Elmendorf et al. 2012, Bjorkman et al. 2020). Less is known about effects of warming on the soil microbial communities despite their important roles in decomposition and nutrient cycling. Warming can directly impact microbial biomass by promoting or demoting microbial growth, with different processes involved such as substrate depletion, differential temperature sensitivity or variation of growth efficiency (Bradford 2013; Walker et al. 2018). In tundra soils, fungal and/or bacterial biomass response to warming has varied greatly between studies, with some studies showing either an increase or decrease (Clemmensen et al. 2006; Yergeau et al. 2012; Rinnan et al. 2011; Rinnan et al. 2013; Chen et al. 2015; Christiansen et al. 2017) while others show no change (Jonasson et al. 1999; Sistla et al. 2013; Xu and Yuan 2017). These discrepancies may be related to the extent to which vegetation shifted with warming. Since different vegetation types harbor different belowground microbial communities, biomass of various microbial groups is likely affected by shifts in vegetation (Clemmensen et al. 2006; Chu and Grogan 2010).

Most studies only report microbial abundances in the organic soil, excluding the litter layer (e.g. Banerjee et al. 2011; Lee et al. 2013; Buckeridge et al. 2013; Gray et al. 2014). Nevertheless, litter and soil constitute different microbial habitats, and the bacterial and fungal community sizes could be differently affected by warming in litter and soil layers, since the litter microbial community faces larger variation in e.g. water content and temperature, compared to the soil layer. Further, litter and soil layers have generally different chemical composition, with a gradient of more labile to

stable organic compounds from fresh litter to the underlying organic soil, and thus decomposition rates are slower in soil (Berg and McClaugherty 2014). Contrasting litter chemistry between evergreen and deciduous plants could also affect microbial abundances (Berg and McClaugherty 2014). Microbially driven decomposition and nutrient turnover rates have been shown to be modified by warming in a meta-analysis (Romero-Olivares et al. 2017), as well as in arctic ecosystems (Daebeler et al. 2017), but vary greatly depending on the tundra ecosystem type and soil water regime (Jonasson et al. 2001; Zak and Kling 2006). The nitrogen (N) and carbon (C) isotopic signatures are affected by these microbial processes (Šantrůčková et al. 2000; Craine et al. 2015), with preferential accumulation of ^{13}C and ^{15}N isotopes (over ^{12}C and ^{14}N) due to fractionation during microbial processing (Ehleringer et al. 2000; Hobbie and Ouimette 2009). Changes in substrate isotopic signatures therefore reflect changes in the extent and type of microbial processing. Understanding the contrasts in warming responses of fungi and bacteria between litter and soil, and between habitats with different vegetation, could help to predict the consequences of vegetation shifts and soil organic matter stability for arctic ecosystem feedbacks to climate.

The aim of this study was to determine direct and indirect effects of warming on bacterial and fungal abundances in litter and organic soil layers of arctic and alpine tundra. The copy numbers of the bacterial 16S rRNA gene and the fungal ITS2 region were used as an estimate of the bacterial and fungal abundances, respectively. Although microbial gene copy numbers do not equal biomass, they correlate with biomass measurements based on ATP, PLFA and flow cytometry (Zhang et al. 2017), and are good proxies of biomass (Rousk et al. 2010, Blagodatskaya and Kuzyakov 2013). Quantitative PCR of marker genes are therefore a tractable approach when processing a high number of samples. To search for generalizable effects, 16 warming experimental sites with open-top chambers (OTCs) across 12 locations across the Arctic were sampled. Here, we tested whether i) microbial abundances in the litter layer respond more to environmental differences and

experimental warming than microbial abundances in the soil layer, ii) the dominant vegetation type (evergreen or deciduous) has an impact on how the microbial abundances respond to experimental warming, and iii) experimental warming affects the relationships between microbial abundances and soil and litter N and C isotopic signatures, as indicators of changed elemental cycling.

MATERIALS AND METHODS

Study sites and sample collection

Litter and soil samples were collected from 16 warming experimental sites that use a passive warming design with open-top chambers (OTCs) that raise the mean summer air temperature (1-3 °C according to Henry and Molau (1997) and 0.5 to 2°C according to Bokhorst et al. (2013). The experiments have been running 7-25 years as part of the ITEX network (https://www.gvsu.edu/itex/) and are located at 12 locations across the arctic or alpine tundra (Supplementary Table S1). The OTCs and control plots are either randomly distributed at the sites or are paired in randomly distributed blocks with a minimum of 4 replicates in each site. To differentiate experimental sites within the same location, experimental sites were named according to the dominant vegetation type (Supplementary Table S1). Site names were abbreviated with the three first letters of the site name, followed by “ev” for evergreen, “de” for deciduous, and “gr” for grass to indicate dominant vegetation. Sites in Endalen were named End_ev_cas and End_ev_dry for dominance by *Cassiope* and *Dryas,* respectively.

Litter and soil were sampled during July and August 2014, with the exception of Alexander fjord in Canada that was sampled in August 2015. Three cores (Ø 3 cm) were taken randomly from each of

the control and OTC plots to a maximum of 20 cm depth, or less depending on the soil layer thickness. Samples were kept at a temperature below 4°C during transportation from the field to the laboratory in Uppsala. All the samples were received within a week. The litter, organic and mineral soil layers were separated for each of the three cores per plot, and material from the same layer was pooled (mineral soil was not included in this study). Larger stones and roots (>5 mm diameter) were removed, the material homogenized thoroughly, weighed and then split into two sub-samples; one kept at -20°C and one freeze-dried and further homogenized by grinding. Gravimetric water content (%) was determined after freeze-drying. The 276 freeze-dried litter and organic soil samples (5-30 mg) were analyzed for C and N content and $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios using an Isoprime isotope ratio mass spectrometer with continuous flow (Isoprime Ltd., Cheadle Hulme, UK) coupled to a Eurovector CN elemental analyzer (Eurovector SPA, Redavalle, Italy).

Quantitative PCR

DNA was extracted in duplicates using the NucleoSpin Soil extraction kit (Macherey-Nagel, PA, USA) from 50 mg of freeze-dried litter or soil (138 samples for each layer), following the manufacturer's instructions. DNA was quantified with a Qubit ® fluorometer and the Qubit® dsDNA BR kit (Life Technologies, USA), duplicates were pooled and then stored at –20 °C. The total abundances of fungi and bacteria were assessed by quantitative PCR (qPCR) of ITS2 and the 16S rRNA gene, respectively. The ITS2 region was targeted using the forward primer gITS7, and a mixture of reverse ITS4 and ITS4a primers at a proportion of 3:1 (Ihrmark et al. 2012; Kyaschenko et al. 2017), and the V3-V4 region of the 16S rRNA gene was targeted using the forward pro341F and reverse pro805R primers (Takahashi et al. 2014). Primers and amplification conditions are detailed in Supplementary Table S2. Quantifications were performed twice on different qPCR runs in 15 µl reactions using the Biorad CFX Connect Real-Time System (Biorad laboratories, CA,

USA). For one sample, the quantification was repeated because the duplicate runs differed by more than one cycle unit (1 Cq). The standard curves were obtained using serial dilutions of linearized plasmids with the cloned fragments of the target gene. Each reaction contained 1X iQ SYBR Green Supermix (Bio-Rad Hercules, CA, USA), 0.5 μg μl^{-1} of BSA and 10 ng of template DNA. Primer concentrations were 0.5 μM in both assays. Tests for PCR inhibition were performed for all samples by amplifying a known amount of the pGEM-T plasmid (Promega, USA) with the plasmid specific T7 and SP6 primers in the presence of 10 ng of template DNA or water. No inhibition was detected.

Statistical analysis

Environmental variables (water content (%), N and C stocks (g m^{-2}), C:N-ratio, pH [soil only]) were checked for multicollinearity. N and C stocks in both soil and litter layers were highly correlated and therefore the C stock was used as a proxy for the N stock. Environmental variables and microbial abundances were tested for homoscedasticity and linearity using the Bartlett and Shapiro tests, respectively, and transformed (log, square root or Box Cox) when needed prior to statistical tests with linear assumptions.

Linear mixed effect models (LMEMs), using the experimental site as random variable, and with independent litter and soil parameters fitted using the lme4 package (Bates et al. 2014) were used to determine the effects of i) warming treatment and litter or soil variables on the microbial abundances, and ii) warming treatment and microbial abundances on soil and litter C and N isotopic signatures across all sites. The P-values were calculated using the lmerTest package with default settings (Kuznetsova et al. 2017), or for interaction terms with type III ANOVA with Satterthwaite's method. The model residuals were checked graphically and using the Anderson-Darling test. For a

few models, one or two entries leading to extreme residuals were removed to improve the linearity of the residuals.

Response ratios (RRs) were calculated as the logarithmic ratio between the mean in warming treatment divided by the mean in the control for each site and for each variable. Confidence intervals of the RRs were calculated according to Hedges et al. (1999) with the adjustment described by Lajeunesse (2011) for paired correlated treatment and control means. Euclidean distances calculated among RRs relative to microbial abundances were clustered using updated Ward's Minimum Variance method implemented in vegan (Oksanen et al. 2013). Positive or negative responses were considered significant when 95 % confidence intervals were not crossing zero. Analysis of variance (ANOVA) of linear model fits were used for testing the significance of the relationships between microbial abundance RRs and initial litter and soil parameters in control plots. One-way ANOVA was used to compare variable means across the sites and warming treatment.

RESULTS

Overall patterns of fungal and bacterial abundances in litter and soil

Taking all experimental sites together, the abundances of both bacteria and fungi were higher in the litter than in the underlying soil layer (Figure 1A). As an average, $1.7 \times 10^9 \pm 1.3 \times 10^9$ ITS copies g^{-1} and $4.3 \times 10^9 \pm 2.1 \times 10^9$ 16S rRNA gene copies g^{-1} were detected in the litter, and $2.7 \times 10^6 \pm 1.7 \times 10^6$ ITS copies g^{-1} and $1.6 \times 10^7 \pm 6.7 \times 10^6$ 16S rRNA gene copies g^{-1} in the soil (mean ± SD). The abundances in control and warming were similar for both layers (Figure 1A). Similarly, the

dominant vegetation type had no influence on the microbial abundances (Figure 1B). Instead, microbial abundances were significantly different among experimental sites for both layers (Figure 1C). The site also structured the litter and soil variables in both layers (Supplementary Figure. S1, one-way ANOVAs, $p<0.001$). The means of the litter and soil variables did not significantly differ in the warming treatment compared to the control across all experimental sites (LMEM, $p>0.05$). The exception was the litter C stock (g m^{-2}), which increased significantly with experimental warming, when variation among experimental sites was accounted for by including site as random factor in the model (LMEM, $p<0.05$).

In the litter layer (Table 1), a highly significant and negative effect of litter C:N on bacterial community size was observed ($p<0.001$), while the effect on fungal abundances was positive ($p<0.01$, Table 1). In experimental sites dominated by evergreen shrubs, stronger effects of C:N and C stock on both litter bacterial and fungal abundances were observed compared to the overall analysis. In contrast, no significant effect was detected in deciduous dominated experimental sites (Table 1). In the soil, C:N was positively related to the fungal community size, particularly in the evergreen vegetation, but not to the bacterial community size. Soil pH affected bacterial abundances positively, but particularly so in the deciduous vegetation, while the fungal abundance was negatively associated with soil pH in the evergreen plant communities (Table 2). Soil water content, unlike the litter water content, was the main driver of soil bacterial abundance in both evergreen and deciduous shrub dominated sites, although more profoundly at sites dominated by deciduous shrubs. By contrast, fungal abundances were only positively associated with water content in deciduous experimental sites. The soil C stock positively affected fungal abundances in sites dominated by evergreen shrubs and overall bacterial abundances across all sites (Table 2). In both layers, the interaction of the warming treatment and the duration of warming was tested and revealed no significant effect.

Site-dependent warming effects

There was no directional effect of warming on microbial abundances, but local warming effects on microbial abundances and litter or soil variables were detected in all experimental sites using response ratios (RRs, Figure 2). Although most of the variation in litter and soil variables associated with microbial shifts were site specific, a cluster analysis differentiated two general types of responses to experimental warming based on microbial abundance RRs (Supplementary Figure S2). One included sites with at least one microbial abundance variable that decreased significantly with warming (Figure 2A), and the other included sites with at least one microbial variable that increased significantly with warming (Figure 2B).

In Adv_gr, Atq_ev, Aud_de, Bar_ev and Pad_ev, a significant decrease of litter fungal abundance with warming was observed, and was associated with a higher litter C stock in the two latter (Figure 2A). A decrease of litter bacterial abundance was detected in Adv_gr, Ale_de, Adv_de, End_ev_cas, Fin_ev and Zac_e, and accompanied by a decrease of litter water content in Ale_de and Fin_ev. In the soil layer, a lower water content with warming was similarly associated to a decline in bacterial abundances in Ale_de, Kil_de and Adv_de. In two experimental sites (Zac_ev, Atq_ev), a lower soil bacterial abundance was concomitant with a higher C stock, although the opposite trend was observed in Adv_gr, End_ev_cas, Kil_de, and Ale_de. Ale_de was also the only site harboring a decrease of soil fungal abundance with warming.

Four out of five experimental sites with positive responses to warming (Figure 2B) had an increased fungal abundance in the litter layer. In all cases except End_ev_dry, the fungal abundance was also higher in the soil layer. The increases of fungal abundances were associated with higher litter water

content (Dov_de, Dov_ev), or higher C:N in litter and soil (Sor_de and Zac_de), although a contradictory response was observed in another site (Dov_de with lower C:N). In the two Dovre sites and Zac_de, soil bacterial abundances were higher with warming along with soil fungal abundances and soil C stocks.

Overall, the sites with negative responses of microbial abundances to warming were twice as numerous as the positive response group. The two clusters of sites (Supplementary Figure S2) could not be associated with a significant shift in litter or soil parameters with warming (Supplementary Figure S3), as all responses were specific to the site, and there was no association between litter and soil variable RRs and microbial abundance RRs across sites. The linear regressions of microbial abundance RRs against all the initial (i.e. control) litter or soil variables across all sites revealed two significant and positive correlations; namely between bacterial abundance RRs and initial C:N in both litter and soil (Figure 2C). The warming duration was also tested and no significant association was detected.

Microbial abundance effects on C and N isotopic signatures

With site as random factor, a positive effect of warming on litter $\delta^{15}N$ signature was observed, together with a significant negative effect of the interaction term between the warming treatment and the bacterial abundance ($p<0.05$). Thus, only under warmed conditions, the bacterial abundance was significantly and negatively correlated with the $\delta^{15}N$ (Table 3). The $\delta^{13}C$ signature was negatively correlated to the bacterial abundance in both layers, regardless of the warming treatment, but the correlation was stronger in the litter layer ($p<0.01$). When the analysis was done separately for sites dominated by either evergreen or deciduous shrubs, these links between bacterial abundances and C and N isotopic signatures were only detected in sites dominated by deciduous

shrubs (Supplementary Table S3). We found no relationship between fungal abundances and isotopic signatures (Table 3).

DISCUSSION

No overall warming or vegetation type effects, but large layer and site effects

Vegetation changes in the OTCs were documented previously in most of the sites included in this study (Elmendorf et al. 2012). The shorter turnover-time of intact surface litter (up to a decade) as compared to the underlying organic layer that accumulate over decennia to millennia, would suggest faster responses in quantity and quality of the litter pool to changes in plant growth and community composition. This reasoning underpinned our expectation that microbial abundances in the superficial litter layer would be more responsive to experimental warming than those in the underlying organic soil layer. Because the magnitude of warming varies across some of the sampled experimental sites (Bokhorst et al. 2013), we acknowledge that the extent of an experimental warming effect might have not been captured. The variability in magnitude of warming across sites could potentially explain the lack of generalizable effects on fungal and bacterial abundances in litter and soil across our broad range of arctic-alpine experimental sites The lack of generalizable effects of warming on microbial abundances is consistent with an earlier meta-analysis based on microbial biomass N and C (Xu and Yuan 2017), however another meta-analysis concluded that warming increased microbial biomass in tundra (Chen et al. 2015). These discrepancies could be due to different methodologies for biomass estimations (e.g. DNA *vs*. cell-based methods) or site selection, especially for tundra sites which are only a subset within the meta-analyses mentioned above. When site variation was accounted for, a warming effect was still not detected on microbial

abundances in either of the layers, neither across all sites nor in sites dominated by deciduous or evergreen vegetation, except for a tendency for a negative warming effect on fungal abundances in evergreen vegetation. (Tables 1 and 2). The only generalizable factor we could identify was that a higher C:N-ratio in the control (and assuming this reflects the initial C:N in the OTC) in both litter and soil resulted in a larger increase of bacteria in the OTCs in relation to the control. The change in C:N ratios suggests legacy effects of vegetation and soil on microbial responses to climate change in tundra ecosystems (Collins et al. 2020).

Across all experimental sites, fungal and bacterial abundances were consistently 2-3 orders of magnitudes higher in litter layers than in soil, which agrees with results based on ergosterol in a subarctic study (Clemmensen et al. 2006). The gene copy numbers per g litter resemble those in earlier studies of litter in arctic systems (e.g. Christiansen et al. 2017), whereas copy numbers in the soils were in the lower range of earlier estimates (Buckeridge et al. 2013; Blaud et al. 2015). The difference between layers likely reflects that high-quality organic matter in the litter layer support larger communities of free-living saprotrophs, similar to what has been observed in boreal forest (Lindahl et al. 2007), whereas the deeper, more energy-depleted organic matter supports smaller microbial communities. A large proportion of microbial communities in deeper soil layers depends on the C inflow from plant roots, either as free-living rhizosphere organisms or as root symbionts, suggesting different functional roles of microbial communities in different layers. The community sizes in each layer, as well as their balance, could thus have functional consequences involving different types and magnitudes of feedbacks between plants and soils.

Within-site responses

A positive effect of warming on litter C stock was detected when site-specific variation was accounted for, which could be linked to enhanced plant growth and vegetation shifts (Callaghan et al. 2004; DeMarco et al. 2014). The positive association between litter mass and bacterial and fungal abundances in evergreen dominated sites shows that larger litter stocks support larger microbial communities. However, the responses of the fungal and bacterial communities were controlled by litter C:N in opposite ways, suggesting a shift from bacterial dominance at lower C:N to fungal dominance at higher C:N (Hu et al. 2001; Drigo et al. 2008). In evergreen vegetation, where the associations were stronger, the shift in bacterial dominance with changing C:N ratios could be exacerbated depending on levels of recalcitrant compounds, favoring fungi over bacteria (Cornelissen et al. 2007; Eskelinen et al. 2009). Although no general effect of warming was detected on soil C stocks, soil C stock, pH and water content associated positively with bacterial abundances, particularly in deciduous-dominated sites. Fungal abundances in soil, on the other hand, were associated with soil C stocks and C:N ratios (positively) and pH (negatively), predominantly in evergreen vegetation. These differences between sites dominated by evergreens or deciduous shrubs suggests that the opposite relationships of bacteria and fungi with C:N observed in the litter layer may propagate to the underlying soil, and may be a longer term process.

The site-specific nature of response patterns for multiple variables was evident, but there were no obvious characteristics that explained response patterns in the individual experimental sites. Nevertheless, there were two types of response ratio patterns, with either bacterial or fungal abundances significantly reduced by warming or significantly increased, but overall, there were more negative than positive effects of warming on response ratios of microbial abundances. Interestingly, an increase in litter mass with warming in some of the sites counteracted a decreased microbial abundance at ecosystem scale in sites with negative response ratios, but exacerbated the positive effects of warming in cases where positive response ratios were accompanied by increased

litter mass. According to earlier vegetation inventories (Elmendorf et al. 2012), those patterns did not consistently relate to shifts in vegetation functional types (eg. deciduous shrubs). However, the role of litter mass in the microbial response to warming would need further investigations, because other litter parameters (e.g. leaf traits, Collins et al. 2020), microbial community composition could interact with the observed local responses of microbial abundances to warming.

Links between microbial abundances and C and N processes

While accounting for the variation attributed to the separate experimental sites, we tested whether microbial abundances and warming could predict stable isotope signatures of C and N in litter and soil. Natural abundances of the stable ^{13}C and ^{15}N isotopes integrate all processes causing isotope fractionation and mixing of various pools (Robinson 2001). Thus, overall changes in stable isotope signatures of a substrate may indicate that the types and magnitudes of C and N cycling processes have been altered, although further evidence is needed for firm conclusions about which processes were affected. Our observations that warming overall increased $\delta^{15}N$ of the litter layer, but that bacterial abundance interacted by reducing $\delta^{15}N$ under warmed conditions, suggests that several processes affecting $\delta^{15}N$ shifted in concert with warming. First, the fact that the increase of $\delta^{15}N$ with warming was only found in the litter layer and mainly driven by sites dominated by deciduous vegetation in which plant communities responded the most (Jonsdottir et al. 2005; Hollister et al. 2005; Ellebjerg et al. 2008; Rinnan et al. 2009; Hudson et al. 2011), suggests that the increase with warming was partly linked to plant-driven changes in litter quality, leading to increased N cycling and loss of ^{15}N-depleted N from the litter N pool. Second, that bacterial abundances could predict the lower $\delta^{15}N$ values under warmed conditions suggests an altered bacterial N cycling at increased temperature. Potentially, the larger communities kept more of the N in their biomass (i.e. increased N use efficiency) resulting in smaller losses of ^{15}N-depleted N. Further work is needed to determine

which processes are affected by warming, as an altered bacterial N cycling could have consequences on ecosystem feedbacks to warming.

Bacterial community size was also associated with decreased $\delta^{13}C$ in both litter and soil, although the effect was strongest in the litter. This pattern was mainly found in sites dominated by deciduous plants. Although microbial biomass typically comprises a small fraction (1-3 %) of soil organic C, practically all plant residue C passes through the microbial biomass at least once as it is transferred from litter inputs to soil C pools with long residence times (Ryan and Aravena 1994). The decomposition process typically leads to a ^{13}C enrichment of remaining C pools and this, together with historic changes in ^{13}C content of the atmosphere, have led to $\delta^{13}C$ increases with depth in soils with limited vertical mixing (Ehleringer et al. 2000; Hobbie and Ouimette 2009). The observed negative relationship between $\delta^{13}C$ and bacterial abundance does not support that increased bacterial activities led to this shift in $\delta^{13}C$. Instead, $\delta^{13}C$ levels could be driven by difference in plant community composition via changed litter quality and decomposition rate (Fernandez et al. 2003) or by variation in drought stress (Welker et al. 1993). Thus, bacterial community abundance was likely an effect of such plant-driven differences across the experimental plots.

To conclude, we found no evidence for an overall effect of warming on microbial abundances in tundra litter and organic soil layers. Instead, we detected a large variation in warming responses across individual sites, with more sites exhibiting negative than positive responses on microbial abundances. Links between microbial abundances and stable isotopic signatures in both litter and soil suggested an altered bacterial processing with warming, especially in sites dominated by deciduous shrubs. Altogether, the results indicate an altered bacterial N-cycling and further research is needed to evaluate its impact on ecosystem feedbacks to climate change.

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TABLE CAPTIONS

Table 1. Prediction of bacterial and fungal abundances in the litter layer by warming treatment and litter properties (water content, C stock, and C:N ratio) using Linear Mixed Effect Models (LMEMs) across all sites, evergreen-dominated and deciduous-dominated sites. Asterisks indicate significant estimates (*** < 0.001; ** < 0.01; * < 0.05; . < 0.1)

Table 2. Prediction of bacterial and fungal abundances in the soil by warming treatment and soil properties (water content, pH, C stock, and C:N ratio) using Linear Mixed Effect Models (LMEMs) across all sites, evergreen-dominated and deciduous-dominated sites. Asterisks indicate significant estimates (*** < 0.001; ** < 0.01; * < 0.05; . < 0.1)

Table 3. Prediction of litter and soil δ13C and δ15N by microbial abundances using LMEMs across all sites. Because of interactions, model fits were evaluated with F-values and associated p-values, calculated using type III ANOVA with Satterthwaite's method and asterisks indicate significant estimates (*** < 0.001; ** < 0.01; * < 0.05; . < 0.1).

FIGURE CAPTIONS

Figure 1. Total bacterial and fungal abundances in the soil and litter layer in A) warmed and control plots, B) sites where the dominant vegetation is deciduous or evergreen shrubs, and C) each of the 16 experimental sites sorted according the dominant vegetation type along the x-axis: deciduous (de) evergreen (ev) or grass (gr). Boxes show the inter-quartile range between the 1st and 3rd

quartiles, with median indicated by the line and whiskers indicate the maximum and minimum of the inter-quartile range.

Figure 2. Warming response ratios (RRs, x-axis) and 95 % confidence intervals of microbial abundances and litter and soil properties at each of the 16 experimental sites. Negative RRs indicate a decrease of the variable with warming and positive RRs indicate an increase. RRs were considered significant when 95 % confidence intervals were not spanning the zero line. A) Experimental sites with at least one microbial variable decreasing with warming, B) sites with at least one microbial variable increasing with warming, and C) linear regressions of RRs of bacterial 16S rRNA gene abundances in soil and litter against C:N ratio in litter of the control plots. ANOVA results of the linear model are presented. Linear models with ITS abundances were non-significant.

Tab1

	Fungal abundances (ITS2 region)					Bacterial abundances (16S rRNA gene)				
	All litter									
	Estimate	SE	df	t-value		Estimate	SE	df	t-value	
Warming	-0.03	0.03	121.16	-1.31		-0.03	0.02	119.49	-1.43	
Moisture	0.19	0.11	127.21	1.81	.	0.14	0.08	129.36	1.79	.
C (g m^{-2})	0.18	0.11	127.93	1.59		0.17	0.08	129.84	2.07	*
C:N	0.29	0.10	132.08	2.81	**	-0.28	0.08	131.90	-3.64	***
	Evergeen litter									
	Estimate	SE	df	t-value		Estimate	SE	df	t-value	
Warming	-0.05	0.03	52.17	-1.71	.	-0.04	0.02	55.80	-1.83	.
Moisture	0.08	0.16	59.00	0.53		0.03	0.11	41.59	0.30	
C (g m^{-2})	0.34	0.13	49.44	2.52	*	0.26	0.08	20.47	3.04	**
C:N	0.54	0.16	57.78	3.49	***	-0.47	0.11	30.57	-4.49	***
	Deciduous litter									
	Estimate	SE	df	t-value		Estimate	SE	df	t-value	
Warming	0.01	0.04	54.48	0.16		0.00	0.04	54.33	-0.08	
Moisture	0.19	0.16	58.73	1.23		0.15	0.13	57.99	1.17	
C (g m^{-2})	0.16	0.18	58.99	0.90		0.17	0.15	58.73	1.15	
C:N	0.21	0.15	55.91	1.43		-0.22	0.12	58.33	-1.81	.

Tab2

	Fungal abundances (ITS2 region)					Bacterial abundances (16S rRNA gene)				
	All Soil									
	Estimate	SE	df	t-value		Estimate	SE	df	t-value	
Warming	0.02	0.02	117.46	0.98		-0.02	0.02	120.48	-0.94	
Moisture	0.12	0.11	102.80	1.09		0.46	0.09	110.37	5.00	***
pH	-0.14	0.10	81.47	-1.50		0.17	0.08	91.85	2.13	*
C (g m^{-2})	0.11	0.12	102.53	0.90		0.20	0.10	110.20	2.09	*
C:N	0.24	0.09	120.61	2.69	**	-0.05	0.07	124.28	-0.71	
	Evergeen soil									
	Estimate	SE	df	t-value		Estimate	SE	df	t-value	
Warming	0.03	0.03	50.41	0.90		-0.02	0.02	48.71	-1.01	
Moisture	-0.09	0.20	44.00	-0.46		0.40	0.16	35.97	2.57	*
pH	-0.34	0.13	22.39	-2.53	*	0.07	0.10	14.41	0.69	
C (g m^{-2})	0.43	0.19	21.38	2.28	*	0.25	0.14	13.68	1.75	
C:N	0.43	0.14	35.44	3.01	**	0.10	0.11	24.54	0.89	
	Deciduous soil									
	Estimate	SE	df	t-value		Estimate	SE	df	t-value	
Warming	0.05	0.03	53.76	1.54		0.01	0.03	52.79	0.30	
Moisture	0.31	0.15	57.87	2.03	*	0.46	0.13	55.97	3.60	***
pH	0.14	0.13	51.17	1.07		0.39	0.12	57.52	3.27	**
C (g m^{-2})	-0.01	0.16	57.50	-0.09		0.26	0.13	57.56	1.96	.
C:N	0.16	0.11	57.41	1.44		-0.17	0.09	55.42	-1.86	.

Tab3

	δ13C						
	Litter				Soil		
	Estimate	Std. Error	F value		Estimate	Std. Error	F value	
Warming	-0.03	0.07	0.24		0.02	0.06	0.16	
Bacterial abundance	-0.33	0.10	9.01	**	-0.13	0.08	6.48	*
Fungal abundance	0.09	0.10	1.00		-0.13	0.08	1.73	
Warming * bacterial abund.	0.05	0.14	0.12		-0.11	0.08	1.95	
Warming * fungal abund.	-0.03	0.13	0.05		0.09	0.09	0.87	
	δ15N						
	Litter				Soil		
	Estimate	Std. Error	F value		Estimate	Std. Error	F value	
Warming	0.13	0.06	5.10	*	0.08	0.06	1.42	
Bacterial abundance	-0.01	0.09	2.16		0.01	0.08	0.15	
Fungal abundance	0.03	0.09	0.38		-0.05	0.09	1.00	
Warming * bacterial abund.	-0.25	0.13	4.00	*	-0.08	0.09	0.81	
Warming * fungal abund.	0.03	0.11	0.07		-0.04	0.10	0.15