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RESEARCH ARTICLE

Subarctic winter warming promotes soil microbial resilience to freeze–thaw cycles and enhances the microbial carbon use efficiency

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Abstract

Climate change is predicted to cause milder winters and thus exacerbate soil freeze–thaw perturbations in the subarctic, recasting the environmental challenges that soil microorganisms need to endure. Historical exposure to environmental stressors can facilitate the microbial resilience to new cycles of that same stress. However, whether and how such microbial memory or stress legacy can modulate microbial responses to cycles of frost remains untested. Here, we conducted an in situ field experiment in a subarctic birch forest, where winter warming resulted in a substantial increase in the number and intensity of freeze–thaw events. After one season of winter warming, which raised mean surface and soil (−8 cm) temperatures by 2.9 and 1.4°C, respectively, we investigated whether the in situ warming-induced increase in frost cycles improved soil microbial resilience to an experimental freeze–thaw perturbation. We found that the resilience of microbial growth was enhanced in the winter warmed soil, which was associated with community differences across treatments. We also found that winter warming enhanced the resilience of bacteria more than fungi. In contrast, the respiration response to freeze–thaw was not affected by a legacy of winter warming. This translated into an enhanced microbial carbon-use efficiency in the winter warming treatments, which could promote the stabilization of soil carbon during such perturbations. Together, these findings highlight the importance of climate history in shaping current and future dynamics of soil microbial functioning to perturbations associated with climate change, with important implications for understanding the potential consequences on microbial-mediated biogeochemical cycles.

KEYWORDS
arctic ecosystems, climate warming, extreme weather events, microbial growth, microbial growth efficiency, microbial respiration, resistance, temperature

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1 | INTRODUCTION

Soil microbial communities are the agents that drive biogeochemical cycles on land (Falkowski et al., 2008). We therefore need to understand how microbial ecology is affected to predict how ecosystems will feed back to climate change (Bardgett et al., 2008; Bradford et al., 2016; Hutchins et al., 2019). Temperature and moisture are two of the strongest rate-regulators of microbial processes and will be powerfully impacted by climate change. In addition to gradual changes in mean temperatures and levels of water availability in soil, climate warming will also cause more frequent and drastic extreme weather events (IPCC, 2021; Reichstein et al., 2013). These changes will impose profound stressors on soil microbial communities, including exposure to cycles of drought interrupted by rainfall, and cycles of freezing followed by thaw (Henry, 2008). Such drying–rewetting and freezing–thawing events are known to induce some of the most violent dynamics in microbial processes and biogeochemical rates ever documented, including a pulse of CO_2 release from soils to the atmosphere (Jarvis et al., 2007; Schimel & Clein, 1996). A major challenge in climate-change ecology is therefore to understand how such perturbations affect soil microbial communities, as these can both directly impact ecosystem functions, and also leave a persistent legacy effect long after conditions have changed (Canarini et al., 2021; Hawkes et al., 2017; Martiny et al., 2017; Ryo et al., 2019; Tájmel et al., 2024).

The historical legacies of drought and drying–rewetting events can affect microbial responses to subsequent perturbations (Evans & Wallenstein, 2012; Hawkes et al., 2017; Li et al., 2018; Meisner et al., 2021; Müller & Bahn, 2022). It has been shown that the ability to recover its state after perturbation—or 'resilience'—of microbial processes to a cycle of drought followed by rewetting can be enhanced by exposure to drought or repeated drying–rewetting cycles in laboratory experiments (Göransson et al., 2013; Meisner et al., 2015, 2017), field experiments (Canarini et al., 2021; de Nijs et al., 2019) and in drier sites along climate gradients (Leizeaga et al., 2021; Tang et al., 2023). How the soil microbial community is able to adapt its traits to recover growth rates faster, and grow with a higher resource-use efficiency—and thus function better under the imposed stress—is intensively debated, but still remains unclear (Allison, 2023; Schimel, 2018). Possibilities include selection for strategies for dormancy (Lennon & Jones, 2011), osmotic regulation to maintain cell rigidity (Warren, 2014, 2022) and the ability to rapidly colonize pulses of resources released during rewetting (Placella et al., 2012). Indeed, the exposure to repeated cycles of drying–rewetting could induce microbial community changes that conferred a higher resilience—faster recovery of growth rates and higher C-use efficiencies—when exposed to new drying–rewetting events (Brangarí et al., 2021), where it was also shown that traits that conferred rapid resource colonization could also favour drought resilience (Hicks, Lin, et al., 2022).

Freeze–thaw cycles impose a similar fluctuation in water availability to a drying–rewetting cycle in soil. That is, when temperatures reach freezing, liquid water is frozen, causing the water potential to fall. As temperatures rise and solid ice thaws, water availability increases again, recovering to the initial condition (Ma et al., 2017; Meisner et al., 2021). Thus, if microbial communities selected through a history of drying–rewetting events will favour characteristics that increase the resilience of microbial growth and C-use efficiency to subsequent drying–rewetting events, the same should be true for the exposure to frost cycles (Li, Xu, et al., 2023), but this has yet to be investigated.

Due to the polar amplification of climate change, subarctic and arctic regions are warming two to four times faster than most other regions, with higher temperatures manifesting particularly as milder winters (IPCC, 2021; Rantanen et al., 2022). One of the major consequences of milder winters is a decrease in the amount and cover of snow (Brown & Mote, 2009), which might induce drastic fluctuations in soil temperature during winter, thereby altering the frequency, intensity and duration of frost cycles (Zhang, 2005). Given the enormous stocks of soil C stored in subarctic and arctic ecosystems and their high sensitivity to climate (Jansson & Hofmockel, 2020; Schuur et al., 2015), understanding the effects of soil freeze–thaw perturbations on microbial processes, as well as their legacies, is crucial for identifying soil C-climate feedbacks at regional and even global scales.

Here, we conducted an in situ winter warming field experiment in a subarctic birch forest, to test the consequences of a milder winter on microbial responses to a freeze–thaw perturbation. The field experiment included a winter warming treatment, which increased surface and soil temperatures and consequently also the occurrence of freeze–thaw events. After one season of the field treatment, soils from winter warmed and control plots were sampled in early spring to test whether the responses of microbial growth, respiration and C use efficiency (CUE) to an experimental cycle of freeze–thaw were affected by a legacy of winter warming. We hypothesized that increased exposure to frost cycles induced by winter warming in the field would favour a composition of microbial traits conferring a higher microbial functional stability to the perturbation (Griffiths et al., 2000; Hicks, Frey, et al., 2022; Schimel et al., 2007), including an acceleration of growth after the perturbation as well as a higher CUE during the perturbation. As a result, we expected that (1) microbial growth would recover faster to undisturbed levels and thus be more resilient to freeze–thaw in the winter warming treatment, and (2) the microbial CUE would be higher after thawing in the winter warmed treatment, thus leading to a smaller loss of soil C via respiration.

2 | METHODS

2.1 | Site description

Soils were sampled from an in situ warming experiment in a subarctic forest near the Abisko Scientific Research Station (68°19′ N, 18°50′ E; 385 m above sea level), located ~200 km north of the

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Arctic Circle in northern Sweden. The soil in the sampled area is a Histosol, rich in organic matter, formed on base-rich schist (IUSS Working Group WRB, 2015), where the organic horizon is 8–25 cm deep. Abisko has a subarctic climate characterized by long, cold winters and short, cool summers, with a mean annual air temperature of 0.4°C, mean annual soil temperature of 2.1°C (at 5 cm depth) and mean annual precipitation of 352 mm (2000–2020 average) (Abisko Scientific Research Station, 2021). The growing season is limited to the frost-free period between June and August. Vegetation at the experimental site is dominated by deciduous shrubs (*Betula pubescens*, *Rubus chamaemorus*, *Salix lapponum*, *Salix glauca*, *Vaccinium uliginosum*, *V. myrtillus*, *V. vitis-idaea*), evergreens (*Cassiope tetragona*, *Empetrum hermaphroditum*), ferns (*Equisetum scirpoides*) and bryophytes (*Pleurozium schreberi*, *Sphagnum* spp., *Hylocomium splendens*).

2.2 | Winter warming experiment and soil sampling

A field warming experiment was established in the summer of 2020, including four replicated blocks. In each block, control and winter warming plots were established (each 1 × 1 m). For the warming treatment, the temperature was manipulated using an infrared heating system that was continuously implemented during the whole winter season, starting on 14 August 2020. The plots were heated from aboveground with IR-heaters (PAS 2, 250W, Backer BHV AB, Sweden) located 1.2 m over the soil surface. The control plots were exposed to ambient conditions.

Data loggers (TMS-4 29cm, TOMST®, Czech Republic) were installed in each plot before the start of the experiment. In situ soil (−8 cm) and surface (0 cm) temperatures, and volumetric soil moisture (between 0 and −14 cm) were monitored with 15 min resolution. On 25 June 2021, after one season of winter warming, five to six soil cores (4-cm diameter × 5-cm depth) were collected from each control and winter warming plot to form homogeneous soil samples (maintaining the original plot replication). All samples were immediately transported to the laboratory, where they were sieved to <4 mm to remove roots and litter debris, and then stored at 4°C until further analysis, or use in experiments (within 4 weeks of preparation). Soil physico-chemical characteristics, including soil organic matter (loss on ignition, at 550°C for 12 h), and total carbon and nitrogen contents, pH and electrical conductivity (1:5, soil: distilled water extraction) were determined (Table 1). Microbial biomass and its community structure were also estimated by the analysis of phospholipid fatty acids (PLFAs) in the sampled soils (Table 1). Microbial PLFAs were extracted from freeze-dried subsamples using the method described by Frostegård et al. (1993) with modifications (Cruz-Paredes et al., 2017). The derived fatty acid methyl esters were quantified on a gas chromatograph with a flame ionization detector. The PLFA biomarkers i14:0, i15:0, a15:0, i16:0, 16:1ω9, 16:1ω7c, 10Me16:0, i17:0, a17:0, 17:1ω8, cy17:0, 10Me17:0, 18:1ω7, 10Me18:0 and cy19:0 were used as indicators for bacterial biomass, and 18:2ω6,9 was used to estimate fungal biomass (Frostegård & Bååth, 1996).

TABLE 1 Effect of winter warming on soil physico-chemical characteristics and microbial phospholipid fatty acid (PLFA) concentrations.

	Control	Winter warming	*p*
Soil organic matter (%)	92.0 (1.0)	89.8 (3.3)	.43
Soil total carbon (%)	43.5 (2.0)	45.0 (1.2)	.35
Soil total nitrogen (%)	1.17 (0.07)	1.11 (0.03)	.31
Soil carbon to nitrogen ratio	37.3 (1.4)	40.5 (0.2)	.10
pH	4.4 (0.1)	4.4 (0.1)	.41
Electrical conductivity ($mS\,cm^{-1}$)	107 (28)	95 (16)	.77
Total PLFAs ($nmol\,g^{-1}$ dry soil)	1191 (62)	1267 (36)	.30
Bacterial PLFAs ($nmol\,g^{-1}$ dry soil)	547 (30)	576 (31)	.48
Fungal PLFAs ($nmol\,g^{-1}$ dry soil)	171 (14)	207 (22)	.15
Fungal-to-bacterial PLFAs ratio	0.31 (0.02)	0.37 (0.06)	.34
G+ bacterial PLFAs ($nmol\,g^{-1}$ dry soil)	161 (9)	166 (6)	.63
G- bacterial PLFAs ($nmol\,g^{-1}$ dry soil)	293 (20)	308 (20)	.51
G+ to G- bacterial PLFA ratio	0.55 (0.02)	0.54 (0.02)	.39
Actinobacteria PLFA ($nmol\,g^{-1}$ dry soil)	23.8 (1.8)	24.5 (1.1)	.76

Note: The values for soils from the control and winter warming treatments are presented as the mean with standard error in parentheses ($n = 4$). Linear mixed-effect models (with the block included as a random effect) were used to test the effect of winter warming on the measured variables.

Gram-positive (G+) bacteria were estimated by the sum of the PLFAs i14:0, i15:0, a15:0, i16:0, i17:0 and a17:0, and gram-negative (G−) bacteria were estimated by the sum of the PLFAs 16:1ω9, 16:1ω7, cy17:0, 18:1ω7 and cy19:0. The PLFAs 10Me17:0 and 10Me18:0 were used to indicate Actinobacteria (Willers et al., 2015). The sum of bacterial PLFAs, fungal PLFAs and unspecific PLFAs (30 in total) was used as a measure of total microbial biomass.

2.3 | Testing the microbial response to a freezing–thawing perturbation

For each of the replicated plots, 1.0 g soil subsamples were weighed into tubes to estimate bacterial growth, fungal growth and respiration in parallel. Half of the samples were frozen at −20°C for 3 days, and then incubated at 20°C (i.e. thawed) for 1 week, during which bacterial growth, fungal growth and respiration were measured at high temporal resolution by destructive sampling (13 time points for each measurement during the incubation; temperature was controlled to 20°C to match the typical air temperature for high summer). The other half of the soil subsamples were kept at 20°C (i.e. never subjected to freezing) as an unperturbed control, and microbial growth and respiration rates of these samples were also measured at the same temporal resolution during the same 1-week incubation.

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2.4 | Microbial analyses

Bacterial growth rates were measured with the ^{3}H-leucine (Leu) incorporation method into extracted bacteria (Bååth, 2001), which uses the tracking of trace concentrations of radioisotopes into bacterial protein during short assays as an estimate of growth rates (Rousk & Bååth, 2011). Briefly, 1.0 g soil subsamples were mixed with deionized water by vortexing for 3 min and centrifuged at low speed (10 min at 1000 *g*). The resulting bacterial suspension was incubated at 20°C with 2 μL 1-[4,5-^{3}H]-Leucine (5.7 TBq mmol^{-1}, Perkin Elmer, USA) and unlabelled Leu with a final concentration of 275 nM Leu in the bacterial suspension. Bacterial growth was terminated after 1 h incubation. After a series of washing steps, the amount of incorporated radioactive label was measured using a liquid scintillation counter. In parallel, thymidine incorporation was measured in a set of samples to determine a conversion factor between leucine and thymidine incorporation, which enabled bacterial growth to be expressed in C units (μg bacterial C production $g^{-1}h^{-1}$) using the empirical relationship determined by Soares and Rousk (2019).

Fungal growth rates were measured by using the modified acetate-in-ergosterol method, adapted for soil (Bååth, 2001; Rousk et al., 2009), which uses the tracking of trace concentrations of acetate into fungal ergosterol as an estimate of fungal biomass production (Rousk & Bååth, 2011). Briefly, 1.0 g soil samples were mixed with 20 μL of ^{14}C-acetate solution ([1-^{14}C] acetic acid, sodium salt, 2.07 GBq mmol^{-1}, Perkin Elmer) and unlabelled sodium acetate, resulting in a final acetate concentration of 220 μM in the soil slurry. Then these samples were incubated for 2 h at 20°C before formalin was added to terminate growth. The ergosterol was then extracted, separated and quantified using high-performance liquid chromatography and the incorporated radioactivity in the collected ergosterol fraction was determined. Fungal growth rates were converted to C units (μg fungal C production $g^{-1}h^{-1}$) also based on Soares and Rousk (2019).

Soil respiration was measured by determining the accumulation of CO_2 in 20 mL headspace vials, which were first purged with pressurized air and sealed with crimp caps, with short incubations for early time points (3–4 h) and longer incubation of later time points (16–24 h), to ensure similar levels of detection. The CO_2 concentration was determined using a gas chromatograph equipped with a headspace autosampler and a thermal conductivity detector.

2.5 | Data analysis and statistics

Microbial CUE was estimated as the ratio between total microbial growth (sum of bacterial and fungal growth, in C units) to the total microbial C use (total microbial growth plus respiration, in C units).

To assess the resilience of microbial communities, we evaluated their recovery time, defined as the time (in h) for microbial growth to recover to the unperturbed level (i.e. the values in non-frozen soils) after thawing. For this, we first normalized the growth rates to the values in non-frozen soils, and then the recovery time was determined by fitting the temporal response of the normalized growth rate reaching 1 with a linear function.

To identify whether in situ temperature and moisture were affected by the field warming treatment, we used linear mixed-effects models (LMMs) with block included as a random effect to test the warming effects on the average soil and surface temperatures and soil moisture both throughout the whole monitoring period and during the soil freezing period. LMMs with block included as a random effect were also conducted to test for differences in soil physico-chemical characteristics and microbial PLFA biomass between control and winter warmed soils. To further test whether the field warming treatment induced a shift in microbial community composition, we performed a principal components analysis (PCA) to screen for differences in the composition of relative abundances (mol%) of PLFAs, then used LMMs with block included as a random effect to test for differences in PC1 and PC2 scores between control and winter warmed soils. We then analysed the effects of winter warming on microbial responses to the freeze–thaw perturbation. LMMs (with block included as a random effect) were conducted to test the fixed effects of winter warming and time on rates of microbial respiration and growth, and the ratio of fungal-to-bacterial growth and CUE. If an overall significant effect of winter warming was detected, post-hoc analyses were performed to identify significant differences between treatments at each time. LMMs were also conducted to test the difference in recovery time between control and winter warming soils. The effects of winter warming and perturbation treatments on cumulative microbial respiration and growth, and mean fungal-to-bacterial growth ratio and CUE were also tested using LMMs (with block included as a random effect). The LMMs were conducted using the 'lme4' package (Bates et al., 2015), while post-hoc comparison of treatments was done using the 'emmeans' package (Searle et al., 2022). All statistical analyses were performed using R (version 4.3.1; R Core Team, 2022).

3 | RESULTS

3.1 | Winter warming increased the occurrence of freezing–thawing events in soils in situ

The warming treatment significantly increased the mean soil (3.2°C in the warming plot vs. 1.8°C in the control plot) and surface (5.0°C vs. 2.1°C) temperatures by +1.4 and +2.9°C, respectively (both $p < .01$; Figure 1a,b) throughout the monitoring period from August 2020 to August 2021. The snow cover in the warmed plots was also reduced compared to control plots. During the winter season, the in situ soil in the control plot (with an average temperature of −0.73°C) was frozen from 30 November to 28 May, while the warming treatment (with an average soil temperature of 0.4°C in this time window) delayed freezing and advanced the thaw timing, with the

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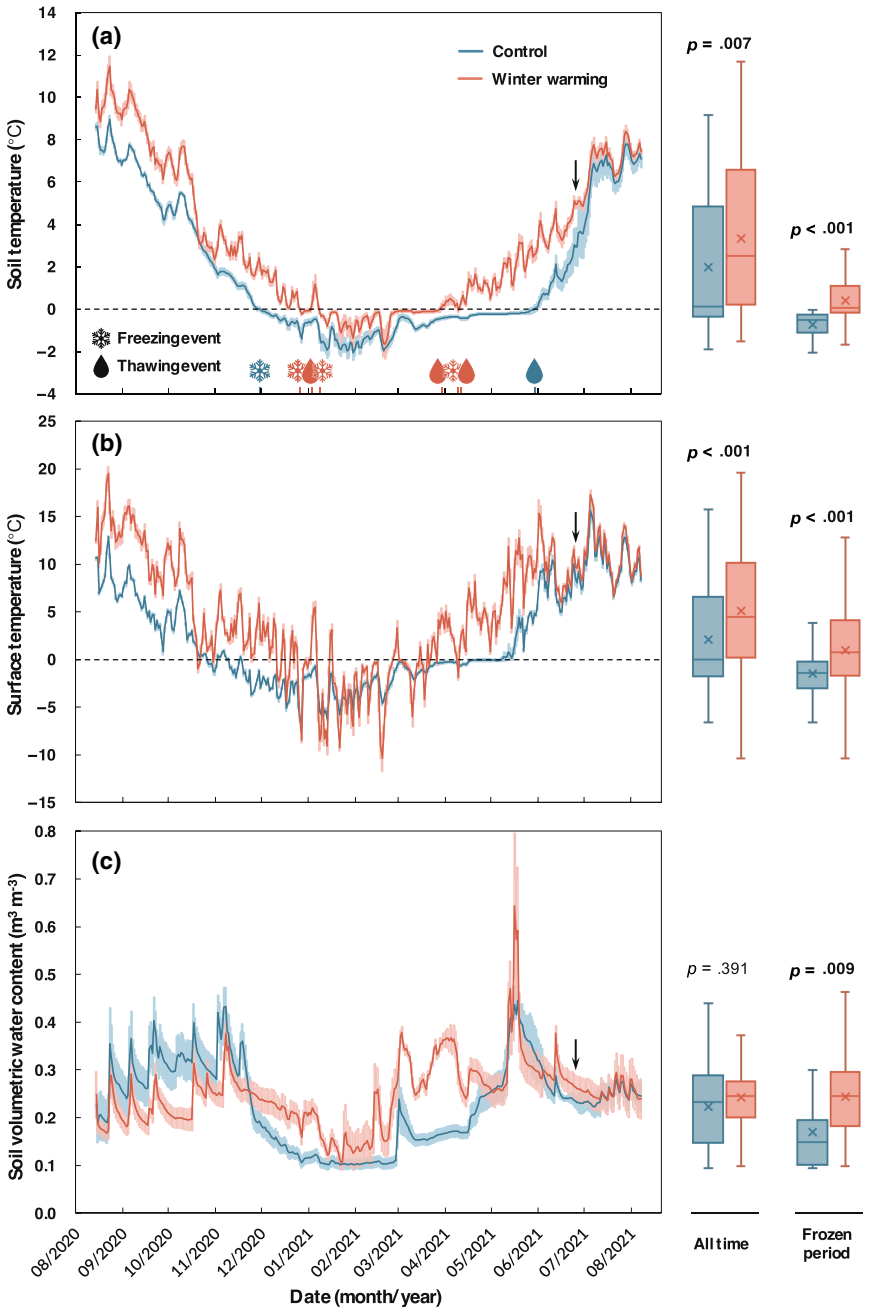


FIGURE 1 Effect of field warming on in situ temperature and moisture. The in situ soil (−8 cm; a) and surface (0 cm; b) temperatures, and volumetric soil moisture (between 0 and −14 cm; c) were monitored from August 2020 to August 2021. The data are the daily mean values, and the shading indicates one standard error among blocks ($n = 4$). The dashed line denotes 0°C as a reference level for freezing. The freezing and thawing events of soil were labelled on the *x*-axis as snowflakes and water drops respectively. Arrows indicate the date on which soils were sampled (25 June 2021). Boxes enclose 1.5 times interquartile range for the temperature and moisture data throughout the monitoring period and during the soil freezing period (from 30 November to 28 May), where the box limits indicate the 25th and 75th percentiles, the whiskers indicate minimum and maximum values, centre lines represent the median values, and the symbols (×) represent the mean (outliers are not shown).

in situ soil experiencing multiple frost cycles between 26 December and 10 April (Figure 1a). Specifically, we observed three freezing events on 26 December, 8 January and 9 April, as well as three thawing events on 3 January, 29 March and 10 April in the in situ soil of the warming plots (Figure 1a). During this time, the soil of the control plots remained frozen.

Although there was no significant difference in average soil volumetric water content between the control (0.23 $m^3 m^{-3}$) and warmed (0.25 $m^3 m^{-3}$) plots throughout the monitoring period ($p = .39$), during the soil freezing period in the control plots (i.e. from 30 November to 28 May, Figure 1a), soil moisture in the warmed plots (with an average of 0.25 $m^3 m^{-3}$) was 42% higher ($p < .01$) and more variable than in the control plots (with an average of 0.18 $m^3 m^{-3}$) (Figure 1c).

3.2 | Winter warming induced a shift in microbial PLFA composition without affecting soil physico-chemical characteristics

There were no significant effects of winter warming on soil organic matter content, carbon and nitrogen contents, carbon to nitrogen ratio, pH, or electrical conductivity (Table 1). However, there was a significant difference in microbial PLFA composition along PC1 between the control and winter warming soils ($p = .03$; Figure 2). The winter warming soil was associated with higher relative abundances of the fungal (18:2ω6,9), gram-positive bacteria (i15:0 and a17:0) and gram-negative bacteria (16:1ω7t) markers (Figure 2). There were no significant differences in total or group-specific microbial PLFA

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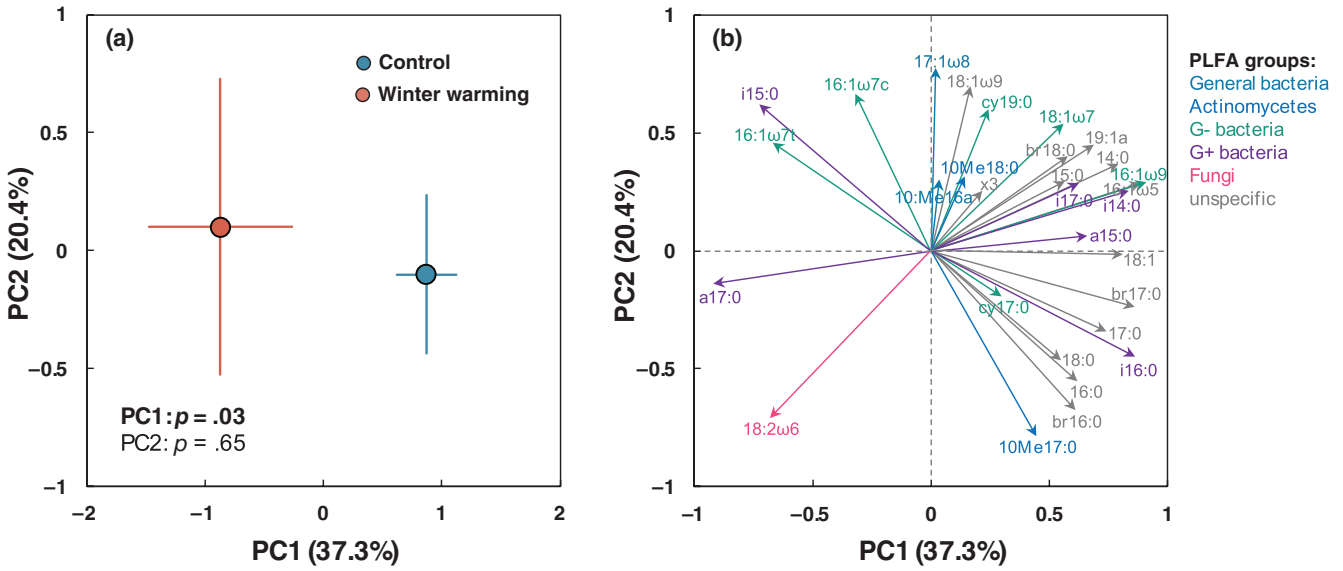


FIGURE 2 The effect of winter warming on soil microbial community composition. A principal component analysis was conducted to summarize the phospholipid fatty acid (PLFA) composition (mol%), with the first two PCs explaining 60% of total variance. (a) Solid points with error bars indicate the mean ± one standard error of scores from the replicated block ($n = 4$). (b) Vector arrows show the loading of individual PLFA biomarkers on each PC axis.

biomass concentrations between the control and winter warming soils (Table 1).

3.3 | Winter warming enhanced microbial growth responses to freeze–thaw perturbation with different effects on bacteria and fungi

Following thawing, bacterial growth rates started increasing immediately and linearly over time to reach a peak (at 43 h for the winter warming treatment, and 73 h for the control soil), before declining to converge with the unperturbed level in both soils (Figure 3a). Bacterial growth recovered significantly faster to levels matching those in unperturbed samples in the winter warming than in the control treatment, with recovery times of 18 ± 5 h versus 38 ± 6 h respectively ($p = .04$; Figure 3b). The freeze–thaw-induced bacterial growth response was also more pronounced in the winter warming compared to the control treatment (Figure 3a), with the maximum bacterial growth rates in the winter warming treatment reaching values (7.4 μg C g^{-1} dry soil h^{-1}) 40% higher ($p = .01$) than the control treatment (5.3 μg C g^{-1} h^{-1}). Compared to the reference levels in the unperturbed samples, the peak value tended to be 16% higher ($p = .18$) in soils from the control treatment, but was 83% higher ($p = .04$) in soils from the warming treatment. Over the 1-week study period, cumulative bacterial growth was not affected by winter warming, the freeze–thaw perturbation or their interaction. However, there was a tendency for freeze–thaw-induced cumulative bacterial growth to be higher in the winter warming treatment (850 μg C g^{-1} dry soil) than in the control (690 μg C g^{-1}; $p = .18$; Figure 3c).

Fungal growth exhibited similar temporal response patterns after freeze–thaw in both the control and winter warming treatments (Figure 2d). The rates of fungal growth recovered linearly from very low values to quickly match those in unperturbed samples (at about 11 h for both soils; Figure 3e), and then kept increasing to reach similar peak levels (c. 1.1 μg C g^{-1} h^{-1}) at 54 h, after which rates converged with the unperturbed level in soils from both field treatments. Compared to the reference levels in the unperturbed samples, the peak value after thawing was 70% higher ($p < .01$) in the control treatment, and 96% higher ($p < .01$) in the winter warming treatment (Figure 3d). The freeze–thaw-induced fungal growth response was more pronounced in the control compared to the winter warming treatment ($p < .001$; Figure 3d). Over the study period, cumulative fungal growth was reduced by winter warming ($p < .01$) but increased by the freeze–thaw perturbation ($p < .001$; Figure 2f). The imposed freeze–thaw cycle enhanced cumulative fungal growth by 40% compared to unperturbed samples in soils from both the control (146 μg C g^{-1} for freeze–thaw treatment, vs. 104 μg C g^{-1} for unperturbed sample, $p < .001$) and winter warming treatments (133 μg C g^{-1} for freeze–thaw perturbation, vs. 95 μg C g^{-1} for unperturbed sample, $p < .001$; Figure 3f). Cumulative fungal growth in the warmed soils was 9% lower than in the control ($p < .001$; Figure 3f).

By summing bacterial and fungal growth rates, it was possible to evaluate the consequence of winter warming on overall microbial growth following the freeze–thaw perturbation. The total microbial growth started increasing immediately and linearly after thawing, reaching a peak (occurring at 43 h in the winter warming treatment, and 73 h for the control) and then converging with the unperturbed level in both treatments (Figure 2g). Microbial growth recovered faster in the winter warming than the control treatment, with recovery times of 18 ± 5 h versus 34 ± 5 h respectively ($p = .046$; Figure 3h). The freeze–thaw-induced maximum

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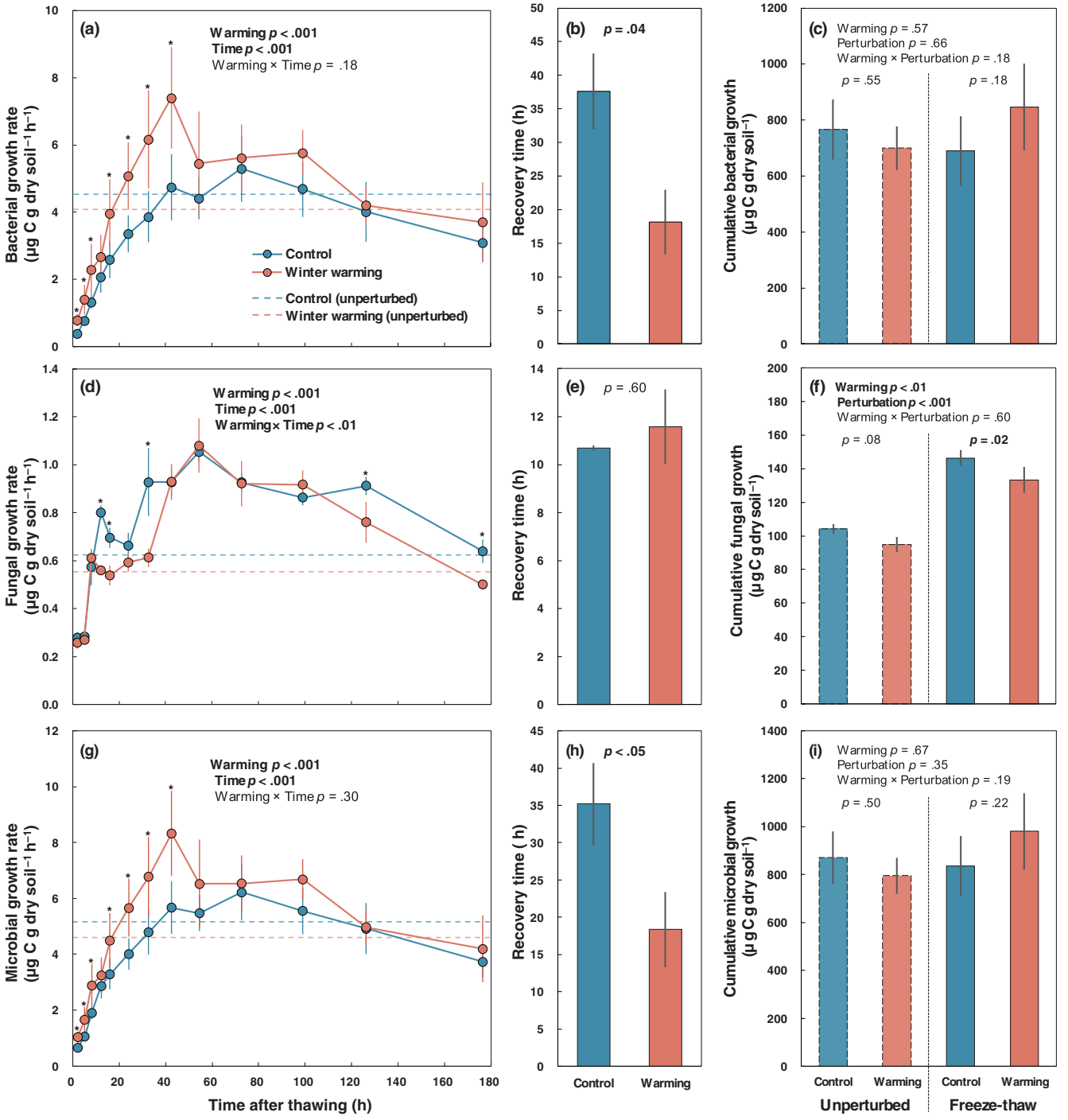


FIGURE 3 The effect of winter warming on the responses of microbial growth to freeze–thaw cycle. (a–c) Bacterial growth; (d–f) fungal growth; (g–i) total microbial (bacterial + fungal) growth. (a, d, g) Temporal dynamics of growth rates after thawing. Asterisks indicate significant differences ($p < .05$) between control and warming treatments at the specified sampling time. (b, e, h) Time taken for microbial growth to recover to the unperturbed level. (c, f, i) Total cumulative growth. The data indicate the mean values, with error bars representing one standard error ($n = 4$). The dashed horizontal lines in panels a, d and g indicate the mean level in unperturbed treatments.

microbial growth rate in the winter warming treatment (8.3 μg $C g^{-1} h^{-1}$) tended to be 34% higher ($p = .054$) than the control treatment (6.2 μg $C g^{-1} h^{-1}$). Compared to the reference levels in the unperturbed soils, the peak in microbial growth was 46% higher in the control treatment ($p < .01$), and 90% higher in the warming treatment ($p < .01$) after the freeze–thaw perturbation. However, there was no significant difference in cumulative microbial growth in soils from the control and winter warming treatments, either in response to freeze–thaw cycle or in the unperturbed soils (Figure 3i).

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3.4 | Winter warming did not affect the response of microbial respiration to freeze–thaw perturbation

Upon thawing, respiration peaked immediately, reaching similar maximal levels within the first 2 h (c. 70 μg C g^{-1} h^{-1}; Figure 4). This respiration peak after the freeze–thaw perturbation was fivefold higher than in the unperturbed soils for both the winter warming and control treatments. Following this, respiration rates decreased exponentially to converge with rates in the unperturbed soils (Figure 4a). Winter warming had no significant effect on either the respiration rate or cumulative respiration after thawing (Figure 4a,b). The freeze–thaw perturbation induced a significant increase in cumulative respiration ($p = .02$; Figure 4b). Compared to the reference levels in the corresponding unperturbed samples, the freeze–thaw cycle tended to enhance cumulative respiration by 21% for the control soil ($p = .12$), and 28% for the warmed soil ($p = .06$) (Figure 4b).

3.5 | Winter warming affected the fungal-to-bacterial growth ratio and microbial CUE during freeze–thaw perturbation

Following thawing, the fungal-to-bacterial growth ratio was initially high (0.8 for the control, and 0.4 for winter warming treatment), being six- and threefold higher than in unperturbed winter warming ($p = .02$) and control ($p = .02$) soils respectively. After this, the fungal-to-bacterial growth ratio gradually decreased to converge with the unperturbed level (Figure 5a). The fungal-to-bacterial growth ratio was significantly lower in the winter warmed (average value of 0.3) compared to control (average value of 0.2) soils ($p < .001$), particularly in the early stage <42 h after thawing (Figure 5a). Compared to the reference levels in unperturbed soils, the freeze–thaw perturbation increased the average fungal-to-bacterial growth ratio, with a more pronounced shift in the control soils (129% increase in fungal-to-bacterial growth ratio; $p < .001$) than the warmed soils (46% increase in fungal-to-bacterial growth ratio; $p = .10$; Figure 4b).

Microbial CUE started from very low levels after thawing, increasing linearly to match levels in the unperturbed soils (~0.27), with slower recovery times of 41 ± 4 h in control treatments compared to 30 ± 6 h in winter warmed soils (Figure 5c). After this, microbial CUE in the warmed soil continued to increase, resulting in a mean CUE (c. 0.32) which tended to be 15% higher ($p = .10$), compared to the unperturbed level 40–120 h after thawing, before slowly declining towards that in the unperturbed samples. While, after recovery, there was no significant difference in CUE between freeze–thaw and unperturbed treatments in the control soil ($p = .41$; Figure 5c,d). Microbial CUE was significantly higher in winter warmed compared to control soils at 24 h ($p = .01$), 33 h ($p = .02$) and 100 h ($p = .04$) after thawing (Figure 5c). There was a tendency for mean CUE to be 11% higher in the freeze–thaw soils (c. 0.27) than in the unperturbed soils (c. 0.30) ($p = .09$; Figure 5d).

4 | DISCUSSION

Past experiences can shape present and future responses of an ecological system (Ryo et al., 2019). The material (e.g. soil C content) or

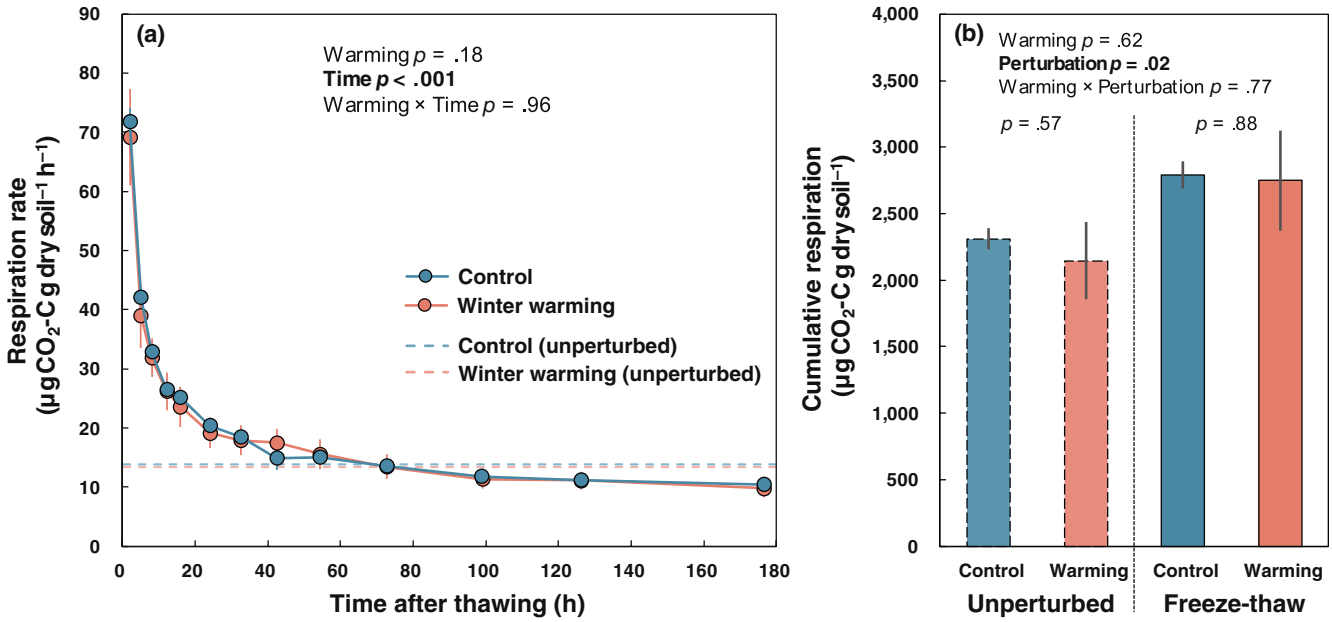


FIGURE 4 The effect of winter warming on the responses of microbial respiration to freeze–thaw cycle. (a) Temporal dynamics of microbial respiration after thawing; and (b) total cumulative respiration. The data indicate the mean values, with error bars representing one standard error ($n = 4$). The dashed horizontal lines in panel a indicate the mean level in unperturbed treatments.

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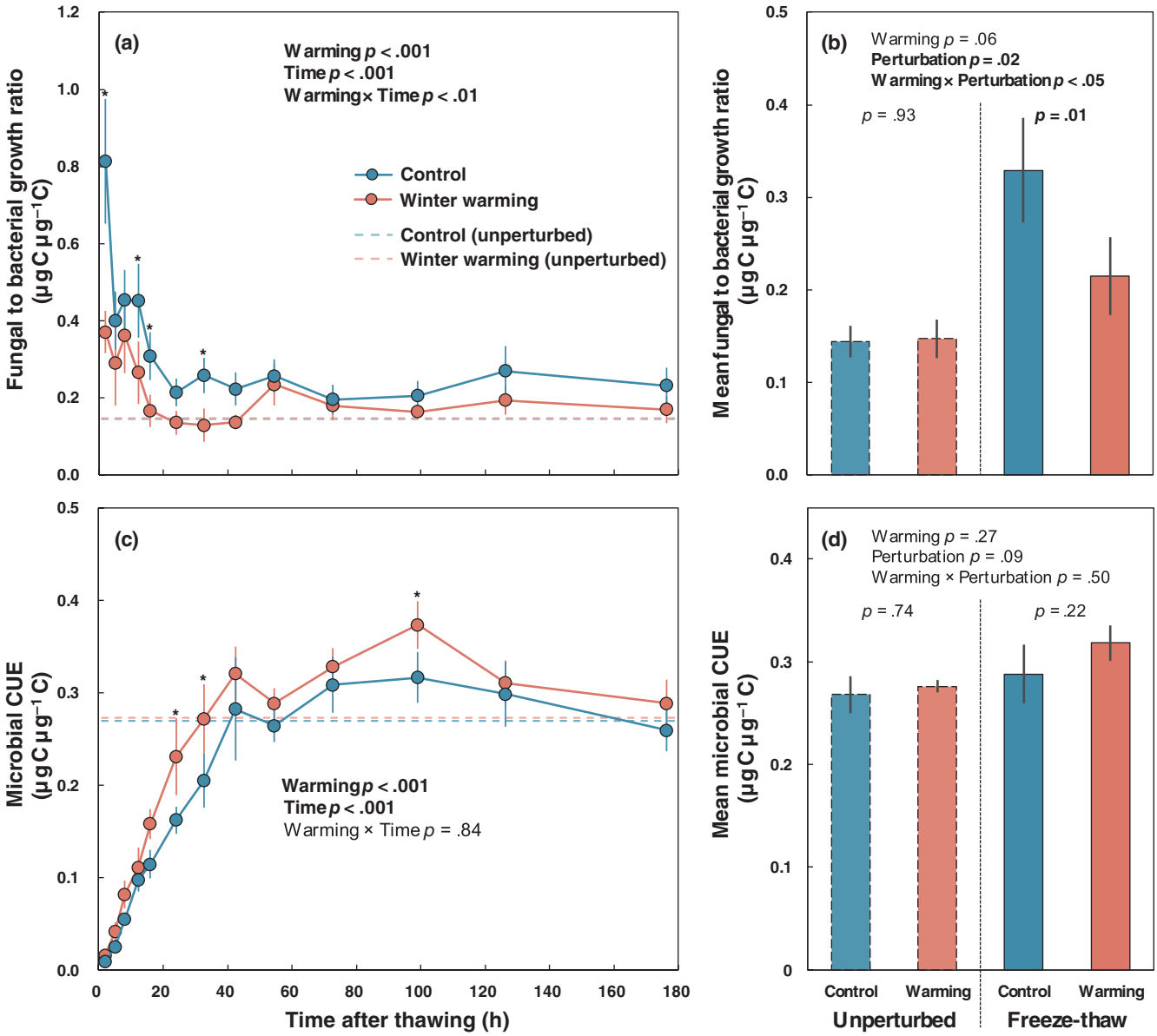


FIGURE 5 The effect of winter warming on the responses of fungal: bacterial growth ratio and microbial CUE to freeze–thaw cycle. (a, c) Temporal dynamics of fungal: bacterial growth ratio (a) and microbial CUE (c) after thawing. Asterisks indicate significant differences between control and winter warming treatments at the specified time. (b, d) Mean values of fungal: bacterial growth ratio (b) and microbial CUE (d) during the incubation. The data indicate the mean values, with error bars representing one standard error ($n = 4$). The dashed horizontal lines in panels a and c indicate the mean level in unperturbed treatments.

informational (i.e. species-associated trait distribution of the community) legacies of past perturbations may lead to the formation of an 'ecological memory', which can influence the ecosystem's ability to cope with subsequent perturbations (Brangarí et al., 2021; Canarini et al., 2021; Johnstone et al., 2016). Given the rising climatic variability caused by global change, understanding such legacy effects will be important for predicting the consequences of microbially mediated biogeochemical cycles in the Anthropocene (Reichstein et al., 2013). Here, we test the consequences of warmer subarctic winters on soil microbial responses to freeze–thaw perturbations to forecast how the soil–atmosphere C balance will be impacted by the ecological memory of warmer winters.

A legacy of drought and drying–rewetting events can enhance the stability and resilience of soil microbial growth and CUE against future perturbations, thus potentially providing a negative feedback to climate change. It was recently found that microbes respond similarly to the dynamics in water potential induced by a freeze–thaw cycle compared to a drying–rewetting cycle (Li, Xu, et al., 2023). Therefore, it is expected that exposure to repeated freeze–thaw cycles will give rise to a microbial community responding with higher growth and CUE resilience to additional freeze–thaw events. The winter warming treatment using IR-heaters clearly increased the number and intensity of frost cycles, as shown by the in situ soil temperature variation (Figure 1a). Thus,

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our field warming experiment provided an ideal platform to test our hypotheses.

4.1 | Increased resilience of microbial growth to freeze–thaw perturbation with divergent responses in bacteria and fungi

Consistent with our hypothesis, we found that the microbial community was more resilient to the imposed freeze–thaw perturbation in the winter warmed treatment, as shown by the faster recovery of microbial growth after thawing (Figure 3g–i). The measured soil physico-chemical characteristics were not affected by the field treatment, thus providing no evidence for abiotic material legacies at the level here resolved (Table 1). The observed formation of an ecological memory was therefore likely caused by shifts in microbial trait distributions induced by the in situ exposure to freeze–thaw cycles in the field, possibly including strategies for dormancy (Lennon & Jones, 2011), osmotic regulation (Warren, 2014, 2022) or the ability to rapidly colonize pulses of resources released during rewetting (Hicks, Lin, et al., 2022; Placella et al., 2012). Such trait distribution shifts that could confer microbial resilience gained from past experiences can be achieved in three ways: physiological acclimation, community shifts and evolutionary adaptation. Even using the limited community resolution provided by PLFA composition shifts, we found a systematic shift in PLFA composition induced by the winter warming treatment, which occurred within one season (Figure 2). This implies that the increased microbial resilience to freeze–thaw perturbation was likely linked to shifts in community composition. More detailed work with higher resolution endpoints will be needed to resolve if specific taxa drove these community trait shifts, but suggestions from comparable experiments on drought cycles (e.g. Malik & Bouskill, 2022; Wallenstein & Hall, 2012) indicate that this is likely.

The winter warming treatment had contrasting effects on the responses of bacterial and fungal growth to the freeze–thaw cycle (Figure 3a,d). Overall, when responding to the freeze–thaw perturbation, bacterial growth benefited from the winter warming field treatment, reaching higher rates faster after thawing (Figure 3a,b), while the fungal growth response to freeze–thaw cycle did not differ between the control and winter warmed soils (Figure 3d,e). Bacterial growth also dominated the response of total microbial growth to the freeze–thaw cycle, with rates of bacterial growth occurring at an order of magnitude higher than fungal growth. In contrast, in the unperturbed state, there was no difference in the biomass (Table 1) and growth (Figure 5b) ratio of fungi to bacteria between the control and winter warmed soils. The freeze–thaw perturbation thus pushed the microbial community towards bacterial dominance in the winter warming treatment (Figure 5a). Taken together, these results highlight a chronic shift towards bacterial decomposers driven by the legacy of winter warming which was evident during the course of the perturbation event itself, emphasizing the biogeochemical role of bacteria during freeze–thaw perturbations, consistent with the recently demonstrated role of bacterial communities during cycles of drought (Malik & Bouskill, 2022).

The divergent responses of bacterial and fungal communities and processes to different environmental constraints have been well documented (e.g. de Vries et al., 2018; Haei et al., 2011; Tian et al., 2021). It is possible that physiological differences between bacterial and fungal decomposers confer different sensitivities to environmental stress (de Vries et al., 2018; Francisco et al., 2019; Guhr et al., 2015; Nagy et al., 2020). We found that the rate of fungal growth recovered to unperturbed level faster than that of bacterial growth (Figure 3b,e), possibly because of the generally greater fungal ability to function under environmental stresses such as osmotic and water potential shifts caused by freeze–thaw perturbations (Harris, 1981; Rath et al., 2016). Fungi are often considered the primary degraders of recalcitrant organic carbon (e.g. lignin) (Janusz et al., 2017; Thevenot et al., 2010), and fungal-derived necromass could preferentially contribute to the formation of more persistent soil organic matter (Clemmensen et al., 2013). Given that fungi and bacteria play different roles in both the degradation and formation of soil organic matter, the divergent responses of microbial communities induced by winter warming are likely to have important consequences for C storage and nutrient turnover in subarctic soils.

Recent work has revealed that the response dynamics of microbial growth to drying–rewetting varies between two extremes: a resilient response ('type 1') where microbes start increasing growth rates immediately with a linear increase over time following rewetting (Iovieno & Bååth, 2008), and a sensitive response ('type 2') where microbial growth increases exponentially but only after a lag period of up to ca. 30 h of near-zero growth (Göransson et al., 2013). The two responses can be regarded as endpoints along a continuous spectrum of differences in microbial resilience, likely related to the drought intensity and perturbation frequency experienced by soil microorganisms in the past (Brangarí et al., 2021; Li, Leizeaga, et al., 2023; Meisner et al., 2017). Prolonged drying can induce a transition towards a more sensitive response to drying–rewetting with a relatively low CUE (Meisner et al., 2015), while exposing soils to repeated cycles of drying–rewetting can shift the response pattern towards a more resilient response with a relatively high CUE (de Nijs et al., 2019; Hicks, Lin, et al., 2022; Leizeaga et al., 2022). In our study, the microbial responses to the imposed freeze–thaw perturbation were all relatively rapid, with increases in growth rate starting immediately after thawing, suggesting a generally high level of resilience to the perturbation. This makes sense given the subarctic study system, which is regularly exposed to freezing and thawing during the seasonal cycle (Figure 1), thus generating an ecological memory enriched by this type of perturbation.

4.2 | Enhanced microbial CUE response to freeze–thaw perturbation

We found clear evidence that the resilience of both bacterial (Figure 3b) and total microbial growth (Figure 3h) were enhanced in the winter warming treatment, resulting in a twofold reduction

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in recovery times. This provides empirical support for hypothesis 1, demonstrating that milder winters will indeed shift microbial trait distributions to confer higher growth resilience. However, the altered microbial growth response to the imposed freeze–thaw cycle was not accompanied by any detectable change in respiration responses. The differential legacy of field winter warming treatment on the responses of microbial growth and respiration to the imposed freeze–thaw cycle resulted in a higher microbial CUE in the winter warmed soil during the perturbation. As soil microbes decompose soil organic matter, they assimilate C, allocating a fraction to growth, and releasing the remaining as CO_2 through respiration (Walker et al., 2018), defining the microbial CUE. This parameter has important implications for the soil–atmosphere C balance by determining the strength of the microbial C pump (Allison et al., 2010; Liang et al., 2017; Manzoni et al., 2012; Tao et al., 2023). We found that microbial CUE was higher and recovered faster to unperturbed levels in the winter warmed compared to the control treatments, aligning with our third hypothesis. This is consistent with the fact that warming increased exposure to freeze–thaw cycles during winter, and that this selected for an enhanced microbial allocation of C to growth during the course of the perturbation, which could ultimately result in an increased stabilization of soil C (Liang et al., 2017). Theoretical arguments (Bosatta & Ågren, 1999; Manzoni et al., 2012) and some empirical evidence (Frey et al., 2013; Li et al., 2019; Purcell et al., 2022; Qiao et al., 2019; Tian et al., 2023) have suggested that microbial CUE decreases with elevated temperatures because of the increased energy requirements directed to metabolism as a direct effect of warming (Fang et al., 2005; Melillo et al., 2002). Our results add complexity to this issue by suggesting that exposure to increased freeze–thaw cycles, as an indirect effect of warming, will create an ecological memory that will accelerate microbial growth responses and increase microbial CUE during the perturbation, thus slowing soil C loss. If this observation can be validated in the long term, this highlights that both direct and indirect effects of warming will need to be considered when scaling up experimental findings to predict changes in global soil C pools as a result of climate change. Furthermore, to date, most assessments of warming have been conducted with a pseudo stable-state assumption, while we find that the largest effects on microbial CUE occur during brief periods of extreme dynamics. Theory and observations to convert dynamic 'hot moments' to long-term consequences for stable C pools have yet to be developed (Kuzyakov & Blagodatskaya, 2015). Indeed, soil microbial communities and functioning frequently deviate from predictions based on changes in mean climatic conditions without accounting for temporal fluctuations and extremes (Harris et al., 2018; Placella et al., 2012; Zhang et al., 2023; Zhu & Cheng, 2011). Therefore, more studies measuring microbial CUE during the course of perturbation events, along with theoretical development and modelling to upscale such dynamic behaviour (e.g. Brangarí et al., 2020, 2021) are required to improve our understanding of soil C dynamics in the context of increasing climatic variability.

4.3 | Implications for climate projections

Our study shows that a more systematic incorporation of historical climate information in soil biogeochemical models could improve the prediction of complex microbial responses to perturbations and changing climate, and ultimately their consequences for land biogeochemical cycles. Despite the recognized importance of climatic legacy for microbial resistance and resilience to perturbations and extreme events (Canarini et al., 2021; Hawkes et al., 2017; Martiny et al., 2017; Ryo et al., 2019; Tájmel et al., 2024), current models of ecosystem functioning typically consider the soil state and microbial community as static and account only loosely for historical information by applying ad-hoc adjustments of initial conditions (Rahmati et al., 2023). We find that one season's winter warming formed an ecological memory that favoured traits that conferred a faster ability to recover microbial growth rates after thaw and an enhanced the CUE during the perturbation. Such changes will alter climate-C-cycle feedback to frost cycles. Our findings reveal that accounting for the trait distribution of the microbial community and its response to change could allow us to better predict the feedback of biogeochemical cycles to future climate fluctuations and extremes.

5 | CONCLUSIONS

Climate change is projected to intensify soil freeze–thaw perturbations during winter with a reduction in snow cover in the subarctic and arctic regions. We here show that increased exposure to freeze–thaw cycles induced by in situ winter warming created an ecological memory, or legacy, that enhanced the stability and resilience of soil microbial growth to a subsequent freeze–thaw perturbation, likely associated with microbial community composition shifts. We also found that winter warming specifically promoted the resilience of bacterial decomposers more than that of fungi. In contrast with microbial growth responses, respiration responses to freeze–thaw perturbation were not affected by winter warming. Thus, the differential legacy of winter warming treatments on microbial growth and respiration responses to a freeze–thaw cycle resulted in an enhanced microbial CUE in the winter warmed soil during the perturbation. Together, these findings demonstrate the importance of climate history in shaping current and future dynamics of soil microbial functioning and highlight the need to understand both direct and indirect effects of warming, and how dynamic microbial responses to perturbations scale up to changes in C stocks, illustrating that microbial traits will determine whether soils will accelerate or slow climate change.

AUTHOR CONTRIBUTIONS

Jin-Tao Lí: Data curation; formal analysis; investigation; visualization; writing – original draft. **Lettice C. Hicks:** Investigation; supervision; writing – review and editing. **Albert C. Brangarí:** Investigation; supervision; writing – review and editing. **Dániel**

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Tájmel: Investigation; writing – review and editing. **Carla Cruz-Paredes:** Investigation; writing – review and editing. **Johannes Rousk:** Conceptualization; funding acquisition; methodology; project administration; resources; supervision; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The original data for this study are publicly available at: https://doi.org/10.5281/zenodo.8219815.

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