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Effects of temperature increase and nitrogen addition on the early litter decomposition in permafrost peatlands

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ABSTRACT

As one kind of the most important carbon (C) sink in the world, peatlands are sensitive to climate change. The decomposition of litter plays an important role in C fixation and nutrient utilization in peatlands. To reveal the mechanism of response of the litter decomposition to climate warming and the addition of nitrogen (N) in permafrost peatlands, we selected two typical plants, *Eriophorum vaginatum* and *Sphagnum palustre*, in the permafrost peatland of Da Xing'anling Mountains, China, as the research objects and conducted a 54-day litter decomposition experiment at 10 ℃ and 20 ℃. Three N addition treatments (CK: 0 mg N g^{-1}, N1: 2.5 mg N g^{-1}, and N2: 5 mg N g^{-1}) were established. Our results showed that the *E. vaginatum* litter decomposed more quickly than that of *Sphagnum*, and an increase in temperature significantly promoted the litter decomposition and CO_2 emission of *E. vaginatum* and *Sphagnum*. The addition of N promoted the decomposition of *E. vaginatum* litter, whereas the decomposition of *Sphagnum* litter was promoted by the N1 treatment but was inhibited by the N2 treatment. The enzyme activity in both types of litter was inhibited with the increase in temperature. The abundances of bacteria and fungi positively correlated with the decomposition constant and mean CO_2 release rate by *E. vaginatum* and *Sphagnum* litter, indicating that the effects of temperature and N addition on the decomposition of plant litter were primarily regulated by microorganisms. This study provides a theoretical basis to understand and predict the effects of global climate change on the decomposition of plant litter in boreal peatlands.

1. Introduction

As one type of important carbon (C) sink, peatlands play an important role in the terrestrial ecosystem. The permafrost peatland contains 277–302 Pg of C, comprising 14 % of the global soil C pool (Hugelius et al., 2014; Tarnocai et al., 2009). Global climate change will affect the C and nitrogen (N) balance of peatlands in permafrost regions, and temperature is an important factor that affects the change of unstable organic matter in permafrost regions (Liu et al., 2019). The increase in temperature will melt the frozen soil, increase the content of water, stimulate the mineralization of soil N in peatlands (Song et al., 2018), improve the net primary productivity of plants (Finger et al., 2016; Keuper et al., 2017, 2012), produce a large amount of the greenhouse gases CO_2 (Bian et al., 2020) and CH_4 that will enter the atmosphere, and then affect the C sink function of peatlands (Tao et al., 2018; Tarnocai, 2009). N is a limiting nutrient in peatland ecosystems (Bragazza et al., 2007; Xing et al., 2011), and the input of N affects the quality of peatland litter (Song et al., 2017). In general, researchers found that plant growth increased significantly when they were subjected to restrictive nutrition (Feller et al., 2003; Lovelock et al., 2004; Mckee et al., 2007). The decomposition of litter plays an important role in the ecosystem regulation of C fixation and nutrient utilization (Menéndez et al., 2003; Mao et al., 2018), which is an important part of the biogeochemical cycle and closely links the underground and aboveground ecosystems (Trogisch et al., 2016). The rate in decrease of decomposition of litter in peatlands is the basic mechanism by which

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peatlands become C sinks (Nikonova et al., 2018). The accumulation of peat in peatlands is primarily caused by the imbalance of plant production and slow decomposition (Zhang et al., 2019). Among them, *Sphagnum* mosses are dominant in peatlands (van Breemen, 1995). These mosses can resist decomposition and increase the accumulation of peat (Bell et al., 2018). Global warming can affect the composition of peatland plant community, enhance the microbial activity and directly and indirectly affect the decomposition process of plant litter, thus affecting the C sink functions of peatlands (Cornelissen et al., 2007; Mao et al., 2018). Simultaneously, studies show that the addition of N can change the nutrient limitation of microorganisms and enzyme activity in the process of litter decomposition, and affect the competitive balance between mosses and vascular plants, and ultimately affect the function of peatlands to accumulate C (Bragazza et al., 2012). Therefore, the changes in temperature and N nutrition environment may lead to changes in the decomposition process of different types of litter in peatlands, which have an important impact on the accumulation of C and nutrient turnover in peatlands. To more effectively predict the impact of global change on the C sequestration function of peatlands, it is necessary to have a thorough understanding of the process of decomposition of litter under increasing temperatures and the addition of N in peatlands.

The decomposition of litter is affected by both biotic and abiotic factors, including litter quality, decomposer communities, and external driving factors (Manninen et al., 2016; Liu et al., 2017; Song et al., 2018). The temperature sensitivity (Q_{10}) of CO_2 release rate is an important indicator of the decomposition of litter under climate change. Simultaneously, the quantification of temperature sensitivity of the mineralization of litter C is of enormous significance for future research of the effects of climate change on litter decomposition. Previous studies have found that the decomposition of litter is primarily regulated by the initial quality of substrate in response to climate warming, e.g., the contents of cellulose and lignin (Bragazza et al., 2006; Jiang et al., 2014; Liu et al., 2016; Mao et al., 2018). Therefore, it is necessary to understand the initial litter characteristics to compare the decomposition of litter among different plant species.

Microbial and enzyme activities play a key role in the decomposition of litter. Fungi and bacteria are the main causes of decomposition of litter in peatlands (Bragazza et al., 2007). Fungi are aerobic microorganisms, which primarily exist in the topsoil (Nilsson et al., 1992). Bacteria primarily exist as aerobic and anaerobic species in peatlands (Sundh et al., 1997). Fungi are dominant in the early stages of decomposition of litter, because they can utilize the high concentration of N and unstable C in litter (Hu et al., 2017). Moreover, important functional genes involved in N fixation, nitrification and denitrification, such as the *nif*H, *nir*K and *nir*S genes, are particularly important for studying the microbial mechanisms involved in the N cycle. In addition, as types of proteins in the soil that are primarily produced by microorganisms, enzymes play a catalytic role, which is conducive to the degradation of litter and an important driving force of decomposition (Allison and Vitousek, 2004). The response of loss of litter mass caused by different microbial enzymatic activities of different plants vary substantially (Allison and Vitousek, 2004; Waring, 2013; Song et al., 2018), and the increase in temperature may affect the activity of enzymes through its effects on microbial activity, thus, accelerating the decomposition of litter. Therefore, it is necessary to study the activities of enzymes and microbial changes during litter decomposition in more detail to clarify the mechanism of response of the litter decomposition to environment change.

Currently, few studies have explored the response mechanism of different plants in peatlands to climate change and increased nutrients availability from the perspective of CO_2 release and microorganisms in the process of litter decomposition (Mao et al., 2018; Song et al., 2018). Therefore, in this study, we selected and collected two typical peatland plants, *Eriophorum vaginatum* and *Sphagnum palustre*, in Da Xing'anling of Heilongjiang Province, Northeast China, and conducted a 54-day simulation experiment that involved laboratory warming and the addition of N to evaluate the effects of an increase in temperature and the addition of N on the decomposition of litter in peatlands. The purpose of this study was to clarify the difference in sensitivity of litter decomposition to changes in temperature and N nutrient environment and its microbial mechanism. Thus, we evaluated the following questions: (1) What is the difference in the decomposition and sensitivity of *E. vaginatum* and *Sphagnum* litter to temperature, and how does an increase in temperature and the addition of N affect the decomposition of litter by two typical types of plant litter in the peatland? (2) Does the initial quality of litter affect the release of CO_2 during the decomposition of peatland litter under warming and N addition? (3) Does an increase in temperature and the addition of N affect the litter decomposition that is related to the key microbial abundance and enzyme activities in peatlands?

2. Materials and methods

2.1. Site description

The study was conducted on a continuous permafrost peatland (52.94°N, 122.86°E) in the Da Xing'anling Mountains of Northeast China. This region belongs to a cold temperate continental monsoon climate, with an altitude of approximately 467 m. The annual average temperature is –3.9 ℃, and the annual average precipitation is 450 mm. The depth of permafrost active layer is 45–65 cm (Mao et al., 2018). The dominant vegetation in this peatland includes *Eriophorum vaginatum* L., *Vaccinium uliginosum* L., *Chamaedaphne calyculata* L. Moench, *Ledum palustre* L. and *Sphagnum palustre* L. (Song et al., 2018). In this study, we primarily selected the litter of *E. vaginatum* and *Sphagnum* to study the effects of temperature and addition of N on the early stage of decomposition of litter in permafrost peatland.

2.2. Sample collection and incubation

In late September 2019, four sampling plots were randomly selected from typical peatlands in the Da Xing'anling Mountains permafrost region to collect *E. vaginatum* and *Sphagnum* litter. For sample collection, we mainly remove the surrounding excess plants and weeds, then use scissors to cut the roots of *E. vaginatum* to collect *E. vaginatum* litter, and collect surface *Sphagnum* with a shovel and hands. Finally, we take these plant samples to the laboratory to pick out other plants and weeds to ensure the accuracy of the samples. Simultaneously, because the decomposition of *Sphagnum* litter is a continuous process, it is almost impossible to determine when the *Sphagnum* litter begins to decompose. According to previous research (Aerts et al., 2001), we therefore use the brown stem segment located 2–4 cm below the growth tip as a representative of newly deposited garbage (Bragazza et al., 2007). The litter of the same species in each plot was mixed into one sample, dried at 65 ℃ and divided into two parts. One portion of the sample was crushed through a 0.15-mm sieve to determine the initial contents of C, N,

Table 1
Initial quality of *Eriophorum vaginatum* and *Sphagnum palustre* litter. The values are described as the mean ± SE (n = 4). Different letters represent different significance ($p < 0.05$).

Parameter	*Eriophorum vaginatum*	*Sphagnum palustre*
C content (mg g^{-1})	417.8 ± 19.17a	380.72 ± 5.37a
N content (mg g^{-1})	5.54 ± 0.03b	9.39 ± 0.04a
P content (mg g^{-1})	0.51 ± 0.07b	0.88 ± 0.11a
C:N ratio	75.34 ± 3.13a	40.54 ± 0.63b
N:P ratio	11.43 ± 1.58a	11.57 ± 0.67a
C:P ratio	870.67 ± 149.82a	469.87 ± 20.34a
Lignin (mg g^{-1})	67.92 ± 2.23b	101.90 ± 1.63a
Lignin:N ratio	12.25 ± 0.42a	10.85 ± 0.17b
Cellulose (mg g^{-1})	472.05 ± 7.45a	404.63 ± 1.94b

phosphorus (P), lignin and cellulose (Table 1). The other portion of the sample was used for the incubation experiment , in which *E. vaginatum* litter was cut into 2 to 2.5 cm segments.

We incubated the litter of *E. vaginatum* and *Sphagnum* for 54 days at 10 ℃ and 20 ℃ in four replicates (Zhang et al., 2017). The temperature setting mainly considers the possible temperature rise caused by global climate change and the actual temperature change of the sample plot, in which 10 ℃ and 20 ℃ represent the average temperature in the growing season (12 ℃) and July (18 ℃) respectively. Two grams of dried *E. vaginatum* and 1.5 g of *Sphagnum* litter were placed in 500 ml wide-mouth bottles. Simulated N in the form of a solution of NH_4NO_3 was added (Zhang et al., 2017). The concentrations of N that were added were the CK (0 mg N g^{-1}), N1 (2.5 mg N g^{-1}) and N2 (5 mg N g^{-1}). The amount of N that was added was primarily determined by considering the total content of N in the *E. vaginatum* and *Sphagnum* litter and the amount that the addition of N may increase the total content of N in *Sphagnum* (van den Elzen et al., 2018), among which 2.5 mg N g^{-1} and 5 mg N g^{-1} were 25 % and 50 % of the total N content of *Sphagnum*, respectively. A volume of 3 ml and 5 ml in situ swamp water was added to the incubation bottles of *E. vaginatum* and *Sphagnum,* respectively, to inoculate them with microorganisms and enable the litter to absorb water to reach its saturation state. Considering the high rate of microbial respiration during the initial stage of litter decomposition, the sampling frequency was increased during the early stage of incubation (Mao et al., 2018). A volume of 20 ml of headspace gas samples was collected at 1, 3, 5, 7, 9, 14, 19, 26, 33, 40, 47 and 54 days of incubation. The CO_2 concentration in each gas sample was analyzed using an Agilent 7820A gas chromatograph (Agilent Technologies, Carpinteria, CA, USA). After each collection of gas, the bottle was weighed, and the corresponding amount of deionized water was added when the weight was reduced. The amount of CO_2 released was calculated as described by Robertson et al. (1999). The cumulative amount of C released in the form of CO_2 during the decomposition of litter, is calculated by the difference in CO_2 concentration between litter treatment and control treatment (Zhang et al., 2019). After 54 days of incubation, the litter samples were collected to measure their microbial abundance, enzyme activity, and contents of C, N and P.

2.3. Sample analysis

DNA was extracted from 0.1 g plant litter samples using a Fast DNA Spin Kit (MP Biomedicals, Solon, OH, USA) following the manufacturer's instructions. The DNA was quantified using a Nanodrop spectrophotometer (ThermoFisher, Waltham, MA, USA), and the quality of DNA was examined using 1.0 % agarose gel electrophoresis. Each sample was repeated four times to obtain more representative DNA samples. Fluorescence quantitative PCR (7500, Applied Biosystems, Foster City, CA, USA) was used to determine the abundance of bacterial 16S rRNA, fungal ITS, *nif*H, *nir*K and *nir*S gene copies. Specific primers and amplification details are shown in Table S1. The PCR reaction system was 25 μl, including 12.5 μl SYBR buffer (TaKaRa, Dalian, China), 10 ng DNA template, 0.4 μl primer (10 μm), 0.5 μl ROXII (TaKaRa), 0.875 μl 3 % BSA and 0.625 μl dimethyl sulfoxide (DMSO). The plasmid of cloned part of the target gene was serially diluted by 10-fold to obtain the standard curve of each target gene. The abundance of litter microbial target functional genes was calculated based on the standard curve and cycle threshold.

The total C content of litter was determined using a multi N/C 2100 TOC analyzer (Analytik Jena, Germany), and the contents of total N and P of the litter samples were determined using an AA3 continuous flow analyzer (Seal AA3 Analytical, Norderstedt, Germany) after wet digestion with sulfuric acid. The acid washing method was used to determine lignin and cellulose content using a Fibertec^{TM} 2010 cellulose analyzer (Foss, Sweden).

The sucrase activity was determined using 3,5-dinitrosalicylic acid colorimetry. With sucrose as the substrate, 0.1 g of litter was incubated with toluene and pH 5.5 phosphate buffer for 24 h at 37 ℃. At the end of incubation, the amount of glucose produced was measured to characterize the sucrase activity (mg glucose g^{-1} 24 h^{-1}). Moreover, the activity of β-glucosidase was determined by incubating 0.1 g litter with p-nitrophenyl-β-D-galactopyranoside (PNPG) as the substrate, adding pH 6.0 modified universal buffer (MUB) and toluene at 37 ℃ for 1 h (mg *p*NP $g^{-1}h^{-1}$). In addition, using phenyl disodium phosphate as the substrate, the acid phosphatase activity of litter was determined by the colorimetric method of diphenyl sodium phosphate. A total of 0.1 g of litter was mixed with pH 5.0 acetic acid buffer solution and toluene and incubated at 37 ℃ for 12 h, and the content of free phenol was determined to characterize the acid phosphatase activity (mg *p*NP g^{-1} 2 h^{-1}). The activity of polyphenol oxidase was measured using pyrogallic acid as the substrate (mg purpurigallin g^{-1} 2 h^{-1}). Litter samples (0.1 g) were incubated with pyrogallic acid solution at 30 ℃ for 2 h, and disodium hydrogen phosphate citric acid buffer at pH 4.5 was added. The purpurigallic acid was extracted with ether, and the polyphenol oxidase activity was determined.

2.4. Statistical analysis

SPSS 19.0 (IBM, Inc., Armonk, NY, USA) was used for all the statistical analyses. A two-way analysis of variance (ANOVA) and significant difference (LSD) methods were used to analyze significant differences in microbial abundance, enzyme activity and the contents of C, N and P of litters that had been incubated at different temperatures and with different amounts of N. In addition, Pearson correlation coefficients between the CO_2 release rate and litter microbial abundance, enzyme activity and C, N and P content were calculated.

The decomposition constant *k* value was calculated using a single exponential linear regression model (Mao et al., 2018; Trofymow et al., 2002). The specific calculation formula was as follows: $\ln y = a - kt$. Among them, y is the C residue (%); a is the intercept; *k* represents the decomposition constant of litters (the higher the *k* value, the faster the decomposition rate), and t is the litter decomposition time. As the temperature sensitivity of litter decomposition, the Q_{10} value is an important index to describe the change in reaction rate when the temperature increased by 10 ℃ (Zhang et al., 2017). Q_{10} was calculated as follows (Zhang et al., 2017): $Q_{10} = A_{20}/A_{10}$. A_{20} and A_{10} represent the decomposition constant *k* at 20 ℃ and 10 ℃, respectively.

The Q_{10} of litter microbial abundances was calculated as follows (Bai et al., 2017):

$$Q_{10} = \left(\frac{Abundance_{20}}{Abundance_{10}}\right)^{\frac{10}{T_{20}-T_{10}}}$$

where $Abundance_{10}$ and $Abundance_{20}$ are the microbial abundance measured at T_{10} (10 ℃) and T_{20} (20 ℃), respectively.

3. Results

3.1. CO_2 release during litter decomposition

The amount of cumulative CO_2 released during the process of decomposition of *E. vaginatum* and *Sphagnum* litter treated with N1 was higher than that of N2 and CK following incubation at 10 ℃ for 54 days (Fig. 1). The cumulative release of CO_2 during the decomposition process of *Sphagnum* under the N2 treatment was lower than that of the CK treatment. The cumulative release of CO_2 during the decomposition process of *E. vaginatum* litter under different treatments fluctuated to some extent. The cumulative release of CO_2 in the CK treatment was higher than those of N1 and N2 in the early stage of decomposition of *E. vaginatum* litter. The cumulative release of CO_2 from *E. vaginatum* litter under the treatment of N1 was higher than that of the CK at 9 days of incubation, while that in the N2 treatment was higher than that of the control at 33 days of incubation (Fig. 1).

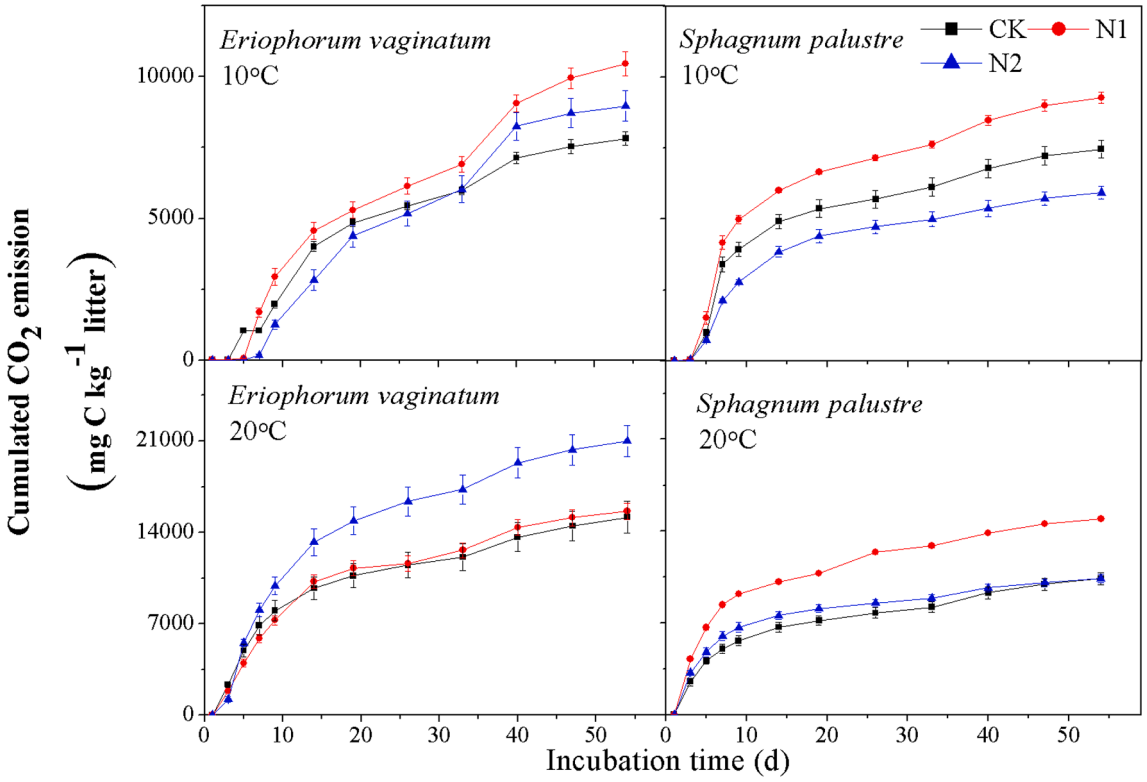

Fig. 1. Effects of warming and nitrogen addition on cumulated CO_2 emission of *Eriophorum vaginatum* and *Sphagnum palustre* litter for 54 days incubation. The CK, N1 and N2 of the nitrogen addition treatmen were 0, 2.5 and 5 mg N g^{-1}, respectively. The values are the mean ± standard error (SE) of each treatment (n = 4).

The increase in temperature promoted the cumulative release of CO_2 during the decomposition of *E. vaginatum* and *Sphagnum* litter (Fig. 1). After 54 days of incubation, the cumulative release of CO_2 from *Sphagnum* litter treated by N1 was higher than those of N2 and CK, while that of *E. vaginatum* under the N2 treatment was higher than those of N1 and CK. With the increase in temperature, the cumulative release of CO_2 from *Sphagnum* litter under the N2 treatment was higher than that of the CK. However, at the beginning, the cumulative release of CO_2 from the *E. vaginatum* litter of the CK treatment was higher than that of N1 and N2, and on the 5th day, the cumulative CO_2 release from *E. vaginatum* litter treated by N2 was higher than that of CK, while on the 14th day, the cumulative CO_2 release from *E. vaginatum* litter treated by N1 was higher than that of CK. The cumulative CO_2 release of *E. vaginatum* litter then tended to be stable (Fig. 1).

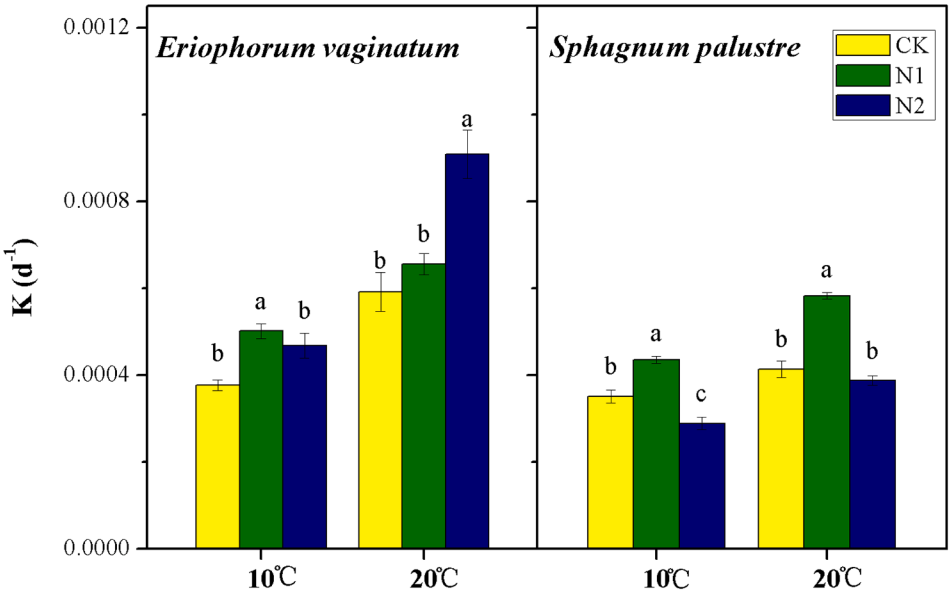

Fig. 2. Effects of warming and nitrogen addition on decomposition constant *k* of *Eriophorum vaginatum* and *Sphagnum palustre* litter for 54 days incubation. The CK, N1 and N2 of the nitrogen addition treatmen were 0, 2.5 and 5 mg N g^{-1}, respectively. The values are the mean ± SE of each treatment (n = 4). Bars with different letters are significantly different ($p < 0.05$).

3.2. Decomposition constants and temperature sensitivity of litter decomposition

The addition of N increased the decomposition constant *k* value of *E. vaginatum* litter, as well as the *k* value of *Sphagnum* litter under N1 treatment, and it was clear for both types of litter in the N1 treatment (Fig. 2). But with the increase of N concentration, N2 treatment reduced the *k* value of *Sphagnum* litter. Warming increased the *k* value of *E. vaginatum* and *Sphagnum* litter, and the *k* value of *E. vaginatum* litter was higher than that of *Sphagnum* litter. With the increase in temperature, N addition increased the *k* value of *E. vaginatum* litter, in which N2 treatment had a significant effect, and N1 treatment significantly increased the *k* value of *Sphagnum* litter, but N2 treatment decreased the *k* value of *Sphagnum* litter. The temperature sensitivity (Q_{10}) of the decomposition of *E. vaginatum* litter was higher than that of *Sphagnum* (Fig. 3). With the increase in concentration of N, the sensitivity of decomposition of the *E. vaginatum* and *Sphagnum* litter to temperature tended to decrease, and the N1 treatment significantly reduced the Q_{10} of decomposition of *E. vaginatum* litter, while the N2 treatment significantly reduced the Q_{10} of decomposition of *Sphagnum* litter, which was the lowest.

3.3. Litter microbial abundance and its temperature sensitivity

At 10 ℃, the abundances of bacteria, fungi, N fixing bacteria and denitrifying bacteria (*nir*K) found in the *E. vaginatum* litter were higher than those of the *Sphagnum* litter (Fig. 4). The addition of N increased the abundances of bacteria, fungi, N fixing bacteria (*nif*H) and denitrifying bacteria (*nir*S) in the *E. vaginatum* and *Sphagnum* litter. The N1 treatment had a significant effect on the abundances of bacteria, N fixing bacteria, fungi and denitrifying bacteria (*nir*K) in the *E. vaginatum* litter. Compared with the N1 treatment, the N2 treatment causes the abundances of bacteria, fungi, *N*-fixing bacteria and denitrifying bacteria (*nirS*) in the *E. vaginatum* and *Sphagnum* litter to decrease slightly, but overall, these values were still higher than those in the CK. The increase in temperature significantly increased the abundances of bacteria, fungi, N fixing bacteria and denitrifying bacteria (*nir*K) in the *E. vaginatum* and *Sphagnum* litter. With the increase in temperature, the N1 treatment significantly increased the abundance of bacteria, fungi, N fixing bacteria and denitrifying bacteria (*nir*S) in the *E. vaginatum* and *Sphagnum* litter, and the related microbial abundance in *E. vaginatum* and *Sphagnum* tended to decrease with the increase in concentration of N. The interaction of temperature and the concentrations of N that were added had a significant effect on the abundance of N fixing bacteria in the *E. vaginatum* litter and bacteria in the *Sphagnum* litter (Table 1). The rate of release of CO_2 positively correlated with the abundance of fungi in the *E. vaginatum* litter, as well as the abundances of bacteria, fungi, N fixing bacteria and denitrifying bacteria in the *Sphagnum* litter. Moreover, based on the diagram of Pearson correlation analysis (Fig. 7), the correlation coefficients between fungal abundance and mean CO_2 release rate of the two litters were higher than those of the bacteria.

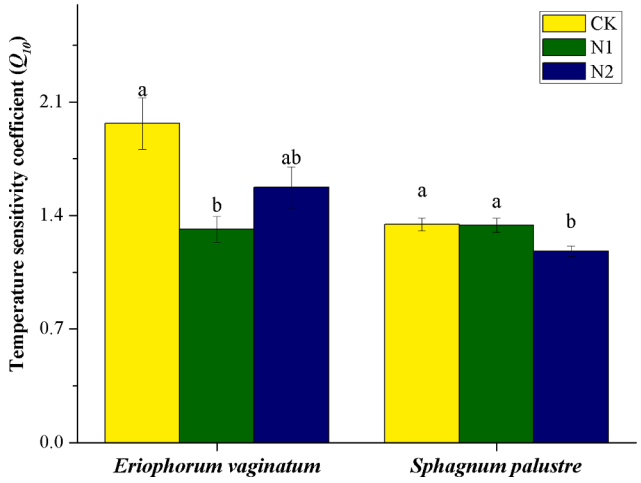

Fig. 3. Effects of warming and nitrogen addition on the temperature sensitivity of litter decomposition of *Eriophorum vaginatum* and *Sphagnum palustre* litter for 54 days incubation. The CK, N1 and N2 of the nitrogen addition treatmen were 0, 2.5 and 5 mg N g^{-1}, respectively. The values are the mean ± SE of each treatment (n = 4). Bars with different letters are significantly different ($p < 0.05$).

The temperature sensitivity of different microorganisms varied. The Q_{10} of the abundance of fungi and N fixing bacteria (*nif*H) in the *E. vaginatum* litter was higher than that in the *Sphagnum* litter, and the temperature sensitivity of the abundance of bacteria in the *Sphagnum* litter was higher than that in the *E. vaginatum* litter (Fig. 5). The Q_{10} value of abundance of N fixing bacteria (*nif*H) in the *E. vaginatum* litter decreased significantly with the increase in concentration of N. The Q_{10} value of abundances of bacteria, fungi and denitrifying bacteria (*nir*K) in the *E. vaginatum* litter increased with the increase in concentration of N that was added. The Q_{10} values of bacterial and fungal abundances in the *Sphagnum* litter decreased significantly with the increase in concentration of N. The N1 treatment reduced the Q_{10} values of the abundances of fungi, N fixing bacteria and denitrifying bacteria (*nir*K) in the *Sphagnum* litter.

3.4. Litter enzyme activities

At 10 ℃, the enzyme activity of the *E. vaginatum* litter was less than that of the *Sphagnum* litter. The addition of N increased the activities of sucrase, β-glucosidase and acid phosphatase in *E. vaginatum* and *Sphagnum* litter, while the activities of polyphenol oxidase decreased (Fig. 6). Moreover, the N1 treatment significantly affected the activities of sucrase, β-glucosidase, acid phosphatase and polyphenol oxidase in the *E. vaginatum* and *Sphagnum* litter. The activities of polyphenol oxidase in the *E. vaginatum* litter, as well as the activities of sucrase, β-glucosidase, acid phosphatase and polyphenol oxidase in the *Sphagnum* litter, significantly decreased as the temperatures increased. With the increase in temperature, the activities of sucrase and polyphenol oxidase in the *E. vaginatum* litter and β-glucosidase in *Sphagnum* litter were significantly decreased by the N1 treatment, and the activities of enzymes in the *E. vaginatum* litter and activities of β-glucosidase and polyphenol oxidase in the *Sphagnum* litter tended to increase. The interaction of temperature and concentration of N had a significant effect on the activities of sucrase in *E. vaginatum* litter and β-glucosidase and polyphenol oxidase activity in *E. vaginatum* and *Sphagnum* litter (Table 2). The rate of CO_2 release negatively correlated with the β-glucosidase activity in *E. vaginatum* litter and the activities of sucrase, polyphenol oxidase and β-glucosidase in the *Sphagnum* litter (Fig. 7).

3.5. Contents of C, N and P in the litters

At 10 ℃, the total C content of the *E. vaginatum* litter was higher than that of *Sphagnum*, and the total N and P contents of the *E. vaginatum* litter were lower than those of the *Sphagnum* litter. The addition of N significantly increased the content of total N of *E. vaginatum* and *Sphagnum* at two different temperatures, and the total N content of both litters increased with the increase in concentration of N that was added. The increase in temperature significantly decreased the total C content of *E. vaginatum* and *Sphagnum* and significantly increased the total P content of *E. vaginatum* and the total N content of *Sphagnum*. With the increase in temperature, the addition of N decreased the total C content of *E. vaginatum* and *Sphagnum*, and the N1 treatment significantly affected the total C content of the *E. vaginatum* and *Sphagnum* litter. Simultaneously, the interaction of temperature and concentration of N that was added had a significant effect on the contents of total C and total N in *Sphagnum* and on the content of total P in the *E. vaginatum* litter. The

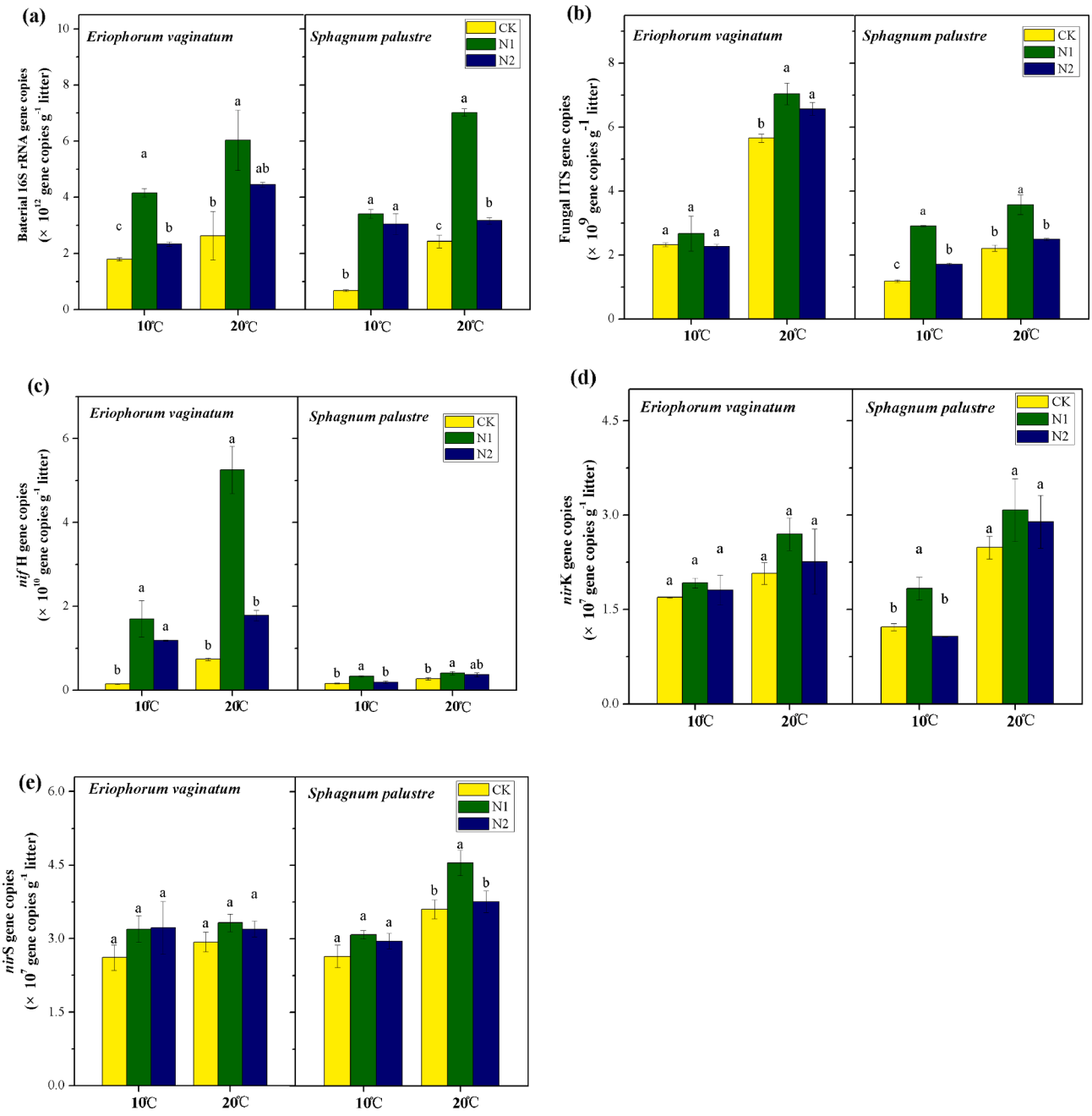

Fig. 4. Effects of warming and nitrogen addition on the microbial abundance of *Eriophorum vaginatum* and *Sphagnum palustre* litter for 54 days incubation. The CK, N1 and N2 of the nitrogen addition treatmen were 0, 2.5 and 5 mg N g^{-1}, respectively. (a) (b) (c) (d) (e) are the abundances of bacteria, fungi, *nif*H, *nir*K, and *nir*S, respectively. The values are the mean ± SE of each treatment (n = 4). Bars with different letters are significantly different ($p < 0.05$).

mean CO_2 release rate negatively correlated with the contents of total C in the *E. vaginatum* and *Sphagnum* litter and positively correlated with the content of total N of the *Sphagnum* litter (Fig. 7).

The N:P ratios of the *E. vaginatum* and *Sphagnum* litter were lower than 14 and 10, respectively, and the N:P ratio of *Sphagnum* litter was lower than that of *E. vaginatum*. The addition of N increased the N:P ratios of *E. vaginatum* and *Sphagnum* litter, and the N1 treatment increased the N:P ratio of *E. vaginatum* litter to a value > 16. The N:P ratios of *E. vaginatum* and *Sphagnum* litter decreased with the increase in temperature, and the N:P ratios of *E. vaginatum* and *Sphagnum* litter increased. The N:P ratios of *E. vaginatum* and *Sphagnum* litter increased with the increase in concentration of N added. The N:P ratio of *E. vaginatum* litter was < 14, while that of *Sphagnum* was > 14 under the N2 treatment (Table 3).

4. Discussion

4.1. Effects of temperature and addition of N on litter decomposition

Warming and N addition can affect the competitive balance among peatland vegetation, stimulate the growth of vascular plants, make *Sphagnum* mosses at a disadvantage in the competition for light (Zeng et al.,2013), and then affect the pattern of peatland vegetation (van den Elzen et al., 2018; Buttler et al., 2015). Therefore, vascular plants may become more dominant in the future (Buttler et al., 2015; Dieleman et al., 2015). In this study, based on the decomposition constant *k* value, we found that the *E. vaginatum* litter decomposed more quickly than the *Sphagnum* litter, which indicated that the decrease of *Sphagnum* and the increase of vascular plants caused by the degradation of permafrost

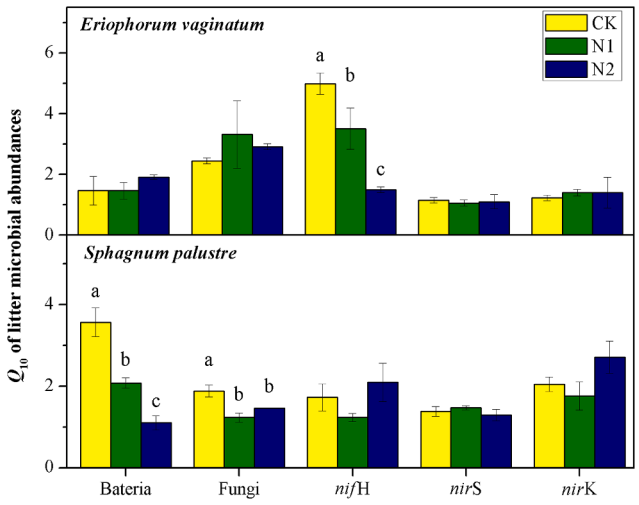

Fig. 5. Effects of warming and nitrogen addition on the temperature sensitivity of microbial abundances between *Eriophorum vaginatum* and *Sphagnum palustre* litter for 54 days incubation. The CK, N1 and N2 of the nitrogen addition treatmen were 0, 2.5 and 5 mg N g^{-1}, respectively. The values are the mean ± SE of each treatment (n = 4). Bars with different letters are significantly different ($p < 0.05$).

would promote the decomposition of litter and loss of C in peatlands (Bragazza et al., 2012). Previous studies in temperate and northern peatlands also showed that the vascular plant litter at 10 ℃ and 20 ℃ decomposed more quickly than that of *Sphagnum* (Dorrepaal et al., 2005; Moore et al., 2007; Mao et al., 2018). In the northern peatland, *Sphagnum* is more adaptable to the harsh environment than *E. vaginatum*, and the vegetation is usually dominated by *Sphagnum* (van Breemen, 1995). *Sphagnum* is the main source of the accumulation of peat, although vascular plants also contribute to it (Zeh et al., 2020). Wang et al. (2018) showed that the litter quality plays an important role during its decomposition by *Sphagnum*. The lower rate of decomposition in *Sphagnum* litter is generally considered to be related to the effects of a low concentration of N (Dorrepaal et al., 2005) and large amounts of lignin and soluble phenolic compounds (Lang et al., 2009). Research by Bu et al. (2011) on peatland bryophytes also showed that the negative reaction of *Sphagnum* to N could benefit the expansion of vascular plants. Vascular plants generally have a higher quality litter as indicated by lower C:N and C:P ratios (Zeh et al., 2020). However, in this study, the litter of *Sphagnum* had a higher concentration of N and a lower C:N ratio than that of *E. vaginatum*, which is consistent with the results of Mao et al. (2018). Our study found that the content of lignin of *E. vaginatum* was lower than that of *Sphagnum*. This result showed that the effect of content of lignin on decomposition was more important than that of the content of N, which verifies that the initial litter quality (lignin content) in our question (2) can affect litter decomposition under warming and nitrogen addition, and further provides additional evidence that the content of lignin of the litter is a powerful indicator of the rate of decomposition of different types of plant litters in permafrost peatlands. Other studies also showed that the content of lignin negatively correlated with the rate of decomposition of litter (Huang et al., 2003).

We found that elevated temperature could significantly promote the decomposition and release of CO_2 of *E. vaginatum* and *Sphagnum* litter, which indicates that the decomposition of litter in permafrost peatland is limited by temperature. Warming can promote the metabolism and activity of microorganisms and accelerate the decomposition of litter (Mao et al., 2018). We found that warming increased the abundances of bacteria, fungi, N fixing bacteria and denitrifying bacteria. Different plants have varying nutrient requirements. The addition of N promoted the decomposition and CO_2 release rate of *Sphagnum* (N1 treatment) and *E. vaginatum* litter, but the N2 treatment inhibited the decomposition of *Sphagnum*. Moderate concentrations of nutrients can promote the

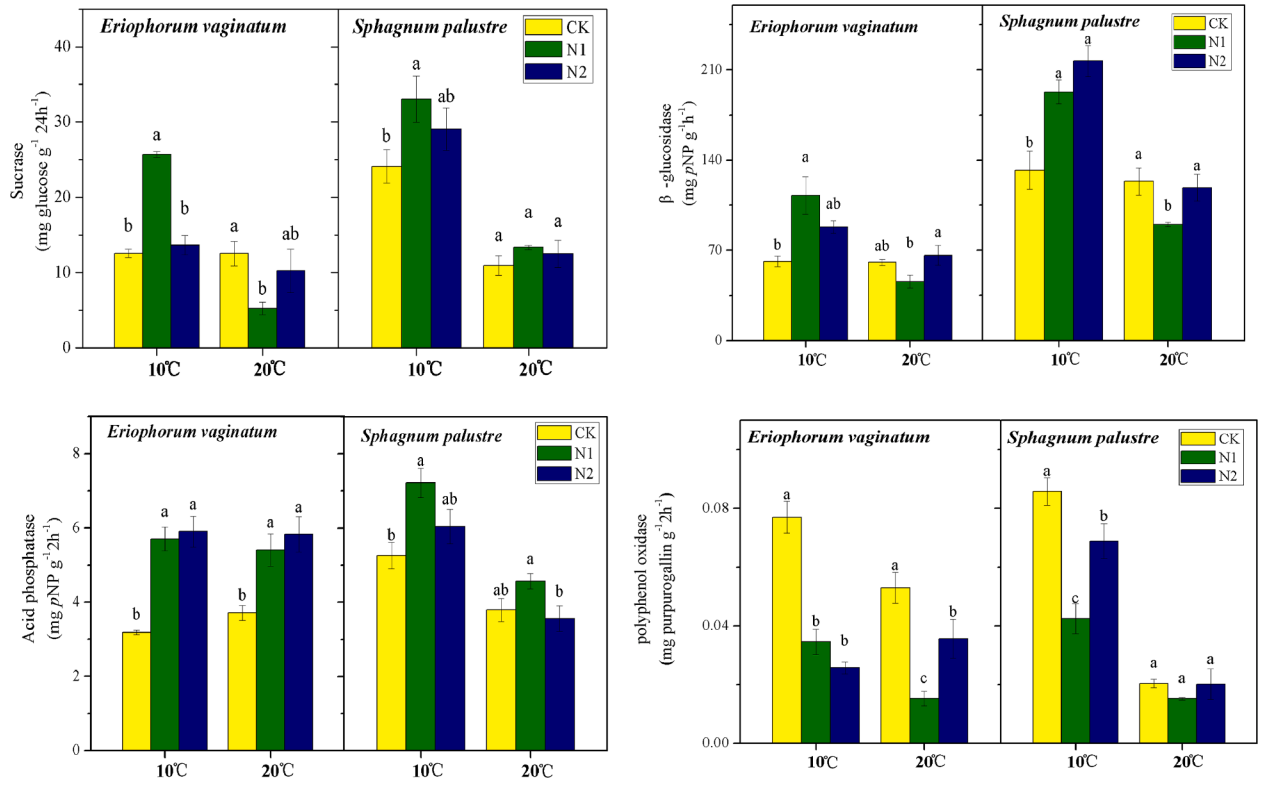

Fig. 6. Effects of warming and nitrogen addition on the enzyme activities of *Eriophorum vaginatum* and *Sphagnum palustre* litter for 54 days incubation. The CK, N1 and N2 of the nitrogen addition treatmen were 0, 2.5 and 5 mg N g^{-1}, respectively. The values are the mean ± SE of each treatment (n = 4). Bars with different letters are significantly different ($p < 0.05$).

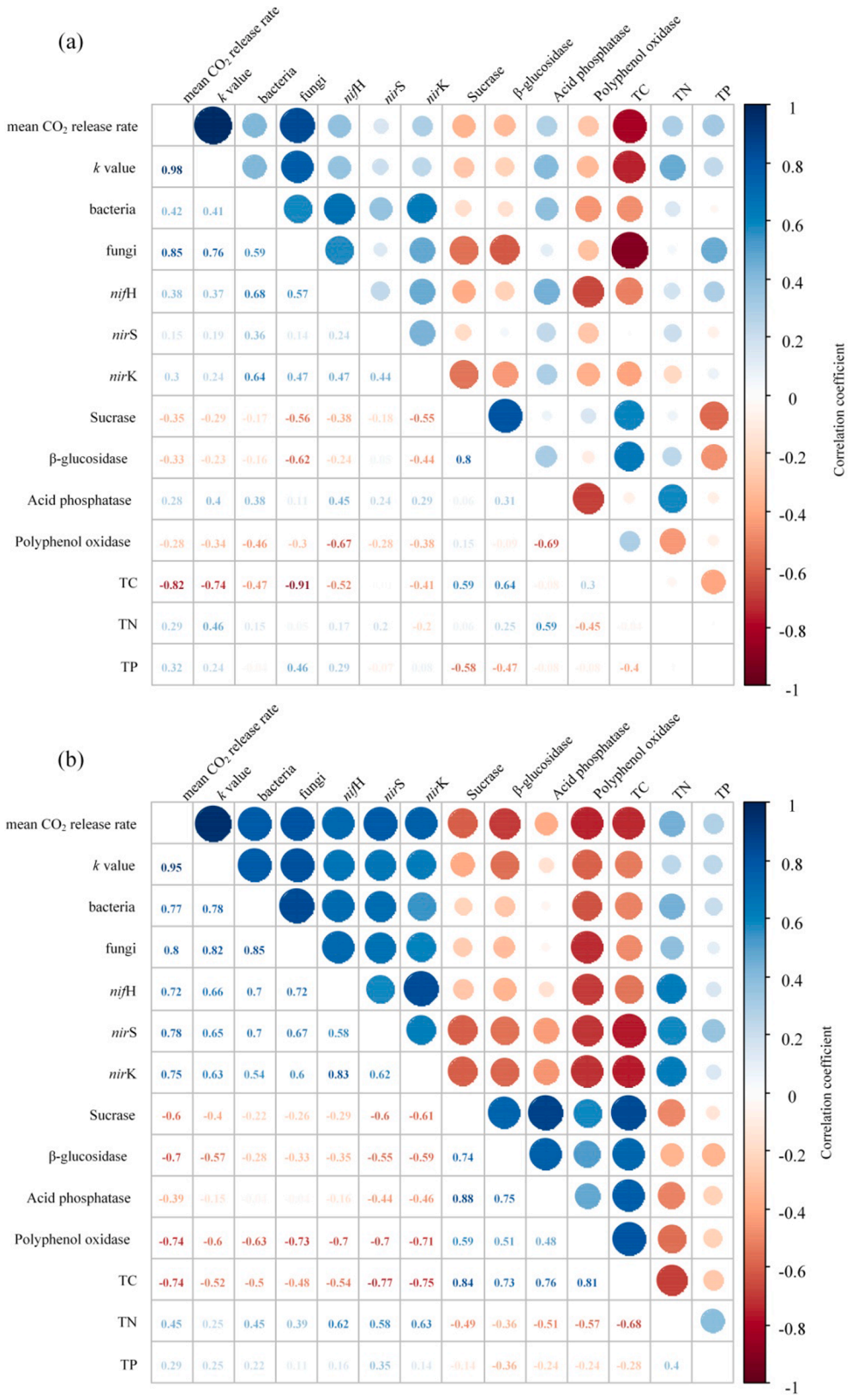

Fig. 7. Pearson correlation analysis diagram. The different size of the circle in different colors represents the size of the correlation coefficient. The deeper the color, the stronger the correlation. Red indicates negative correlation and blue indicates positive correlation. The numbers with different colors in the figure represent the correlation coefficient, (a) and (b) represent respectively *Eriophorum vaginatum* and *Sphagnum palustre*. TC, TN and TP are the contents of total carbon, total nitrogen and total phosphorus respectively.

metabolic activities of microorganisms, which is conducive to the decomposition of litter. *Sphagnum* is well adapted for survival in a low N environment (van den Elzen et al., 2018). An environment with a high concentration of N may not be conducive to the microbial and enzyme activities of *Sphagnum* litter and inhibits its decomposition. Zhang et al. (2017) 's laboratory study on the decomposition of litter in freshwater marshes of Northeast China also showed that *N*-enrichment treatment (25 mg N g^{-1} litter) inhibited the decomposition of litter at 5 ℃ and 15 ℃, which is consistent with our results. This may be because microorganisms have low demand for N in the decomposition process, and the

Table 2
Analysis of variance of effects of warming and nitrogen addition on enzyme activity and microbial abundances of *Eriophorum vaginatum* and *Sphagnum palustre* litter in permafrost peatland.(** indicates a significant correlation at the 0.01 level (two-sided). * indicates a significant correlation at the 0.05 level (two-sided). TC, TN and TP are the contents of total carbon, total nitrogen and total phosphorus respectively.).

		mean CO_2 release rate	bacteria	fungi	*nif*H	*nir*S	*nir*K	Sucrase	β-glucosidase	Acid phosphatase	Polyphenoloxidase	TC	TN	TP
Eriophorum vaginatum	Temperature	161.00**	11.93**	304.72**	42.84**	0.33	6.04*	40.59**	23.94**	0.03	6.58*	89.16**	0.49	14.26**
	Nitrogen addition	9.83**	12.86**	4.73*	54.49**	1.64	1.31	3.03	3.49	27.77**	34.17**	0.61	40.24**	1.57
	Temperature * Nitrogen addition	9.84**	0.70	2.14	16.74**	0.17	0.31	25.61**	10.20**	0.72	6.35**	2.62	1.22	6.82**
Sphagnum palustre	Temperature	328.40**	122.16**	56.39**	22.07**	44.03**	38.09**	89.06**	65.1**	57.45**	159.79**	789.66**	57.52**	1.48
	Nitrogen addition	100.84**	164.71**	70.39**	12.06**	6.29**	2.45	3.53	7.31**	8.18**	12.00**	1.80	23.42**	0.21
	Temperature * Nitrogen addition	10.82**	37.50**	0.92	1.35	1.51	0.66	1.17	12.47**	1.62	9.44**	3.75*	5.71*	0.43

addition of high concentration N may have a toxic effect on decomposers (Ramirez et al., 2012), so it inhibited the activities of decomposers, resulting in a reduction in the decomposition rate. Moreover, high concentration of N addition also could change the P or other nutrient limitation of microorganisms during the process of litter decomposition and further inhibit the decomposition of *Sphagnum* litter (Huang et al., 2021). Simultaneously, the temperature sensitivity Q_{10} value of the decomposition constant decreased with the increase in concentration of N added. However, the litter decomposition constant *k* of *Sphagnum* litter was less sensitive to the increase in temperature than that of the *E. vaginatum* litter, which was consistent with the findings of Mao et al. (2018). This was primarily owing to the high concentration of inhibitory compounds in *Sphagnum* tissue that inhibited the activities of microorganisms (Turetsky et al., 2008), which once again proves that *Sphagnum* mosses are more conducive to the accumulation of peat than vascular plants (van den Elzen et al., 2018).

4.2. Effects of temperature and addition of N on microbial abundance and enzyme activity of plant litters

Microorganisms are important components in the plant-soil material cycle. Studies have shown that temperature and labile substrates can affect the coupling relationship between C and N in peatlands by regulating the response of soil microbial abundance and enzyme activity to warming (Song et al., 2019). Our study found that warming and the addition of N significantly increased the abundance of key microorganisms in the C and N cycle of *E. vaginatum* and *Sphagnum* litter, indicating that warming can enhance the activity of microorganisms (Conant et al., 2011). The addition of N can provide nutrients to microorganisms, accelerate microbial metabolic activities, and then accelerate the decomposition of plant litter in peatland ecosystems. Interestingly, the abundances of bacteria and fungi positively correlated with the *k* value of decomposition constant and the mean CO_2 release rate. This phenomenon further confirmed that bacteria and fungi play important roles in the decomposition of litter (Bragazza et al., 2007). In addition, the correlation coefficients between fungal abundance and the mean CO_2 release rate of the two litters were higher than those of bacteria, which indicate that fungi are more dominant during the early stages of decomposition (Hu et al., 2017). Other studies have shown that the addition of N can significantly change the composition of bacterial community (Craig et al., 2021), and the change in bacterial community structure is accompanied by a change of enzyme activity involved in the C, N and P cycles. Typically, microorganisms can secrete a large array of enzymes, which can significantly promote the decomposition and degradation of litter. In this study, the addition of N enhanced the activities of β-glucosidase, sucrase and acid phosphatase of the *E. vaginatum* and *Sphagnum* litter. Consistent with the results of this study, our previous studies showed that the addition of N significantly enhanced the activities of β-glucosidase, sucrase and acid phosphatase of litter under a field N input experiment (Song et al., 2017). It should be noted that the enzyme activity of *Sphagnum* litter was inhibited with the increase in temperature in this study. A little different from our question (3), the correlation analysis indicated that the activities of β-glucosidase, sucrase and polyphenol oxidase in *Sphagnum* litter negatively correlated with the rate of release of CO_2, which could be owing to the reduction of C substrates caused by the decomposition of plant litter, resulting in the inhibition of enzyme activities.

4.3. Effects of temperature and addition of N on the contents of C, N and P of plant litter

The total C content of *E. vaginatum* and *Sphagnum* litter decreased significantly with the increase in temperature, which was primarily owing to the increase in temperature that stimulated the C demand of microorganisms in the litter (Bragazza et al., 2015). Simultaneously, the addition of N significantly increased the content of total N of *E.*

Table 3
Effects of warming and nitrogen addition on the carbon, nitrogen and phosphorus contents of *Eriophorum vaginatum* and *Sphagnum palustre* litter for 54 days incubation. The CK, N1 and N2 of the nitrogen addition treatmen were 0, 2.5 and 5 mg N g^{-1}, respectively. TC, TN and TP are the contents of total carbon, total nitrogen and total phosphorus respectively. Different letters are significantly different ($p < 0.05$). The values are the mean ± SE of each treatment (n = 4).

		10℃				20℃			
		TC (mg g^{-1})	TN (mg g^{-1})	TP (mg g^{-1})	N:P ratio	TC (mg g^{-1})	TN (mg g^{-1})	TP (mg g^{-1})	N:P ratio
Eriophorum vaginatum	CK	406.62 ± 9.10	5.54 ± 0.20c	0.54 ± 0.06ab	10.55 ± 1.14b	355.75 ± 8.06a	4.71 ± 0.17c	0.67 ± 0.03	4.71 ± 0.17c
	N1	417.31 ± 13.88	6.50 ± 0.02b	0.40 ± 0.03b	16.62 ± 1.54a	323.73 ± 5.85b	6.42 ± 0.39b	0.67 ± 0.03	6.42 ± 0.39a
	N2	416.50 ± 11.01	8.23 ± 0.33a	0.60 ± 0.05a	13.95 ± 1.10ab	330.44 ± 10.02ab	8.52 ± 0.68a	0.58 ± 0.04	8.52 ± 0.68b
Sphagnum palustre	CK	372.28 ± 4.94	8.24 ± 0.26b	0.97 ± 0.08	8.71 ± 0.85b	269.97 ± 1.43a	9.49 ± 0.02a	0.96 ± 0.05	9.96 ± 0.51b
	N1	382.25 ± 6.92	8.93 ± 0.34ab	0.93 ± 0.06	9.64 ± 0.51b	256.82 ± 2.02b	11.76 ± 0.49b	1.08 ± 0.11	11.14 ± 0.85b
	N2	364.05 ± 6.12	9.80 ± 0.37a	0.88 ± 0.06	11.35 ± 0.88a	261.08 ± 4.76ab	14.11 ± 0.81c	1.02 ± 0.16	14.60 ± 1.58a

vaginatum and *Sphagnum*, which was consistent with the results of Song et al. (2018), primarily because the addition of N promotes the fixation of N by microorganisms. We also found that the addition of N had no significant effect on the content of P but had a significant effect on the N:P ratios of two types of litter. The N:P ratio of litter is an important index that reflects the limitation of N and P elements. At the community level of wetland ecosystems, N:P > 16 indicates P limitation; N:P = 14–16 indicates joint limitation of N and P, and N:P < 14 indicates N limitation (Koerselman et al., 1996). Another study also found that for *Sphagnum*, when N:P > 14, it is expressed as P limitation, and when N:P < 10, it is N limitation (Aerts, 1992). We found that at 10 ℃, the N:P ratios of *E. vaginatum* and *Sphagnum* litter were lower than 14 and 10, respectively, and the N:P ratio of *Sphagnum* was lower than that of the *E. vaginatum* litter. This finding indicated that *Sphagnum* was more susceptible to N limitation than *E. vaginatum* at 10 ℃. In addition, the N1 treatment resulted in an N:P ratio of *E. vaginatum* litter that was higher than 16, which showed that the decomposition of *E. vaginatum* litter is limited by P under the N1 treatment. However, with the increase in temperature, the N:P ratio of *E. vaginatum* litter decreased, and the N:P ratio of *Sphagnum* litter increased, indicating that the absorption and utilization of N and P in *E. vaginatum* increased with the increase in temperature. Moreover, with the increase in temperature, the N2 treatment changed the limitation of *Sphagnum* from N to P, which may be primarily owing to the addition of N to meet the microbial demand for N, which in turn, strengthened the P limitation.

5. Conclusion

This study emphasized the differences in early decomposition of *E. vaginatum* and *Sphagnum* litter and their microbial mechanisms in permafrost peatlands under the conditions of warming and N addition. We found that the response of different rates of litter decomposition to the addition of N primarily depends on the initial content of lignin in the litter. Elevated temperatures could significantly promote the decomposition of *E. vaginatum* and *Sphagnum* litter, and the rate of decomposition of *E. vaginatum* is faster than that of *Sphagnum*, indicating that warming is more conducive to the decomposition of *E. vaginatum* litter. The increase in available N promoted the decomposition of *E. vaginatum* and *Sphagnum* litter, but the accumulation of additional N inhibited the decomposition of *Sphagnum* litter. The addition of N enhanced the activities of β-glucosidase, sucrase and acid phosphatase of the *E. vaginatum* and *Sphagnum* litter. With the increase in temperature, the decomposition of C containing substrates in plant litter decreased, resulting in the inhibition of enzyme activities. The abundances of bacteria and fungi positively correlated with the decomposition constant *k* value and mean CO_2 release rate of *E. vaginatum* and *Sphagnum* litter, and the correlation coefficients of fungal abundance and mean CO_2 release rate of the two litters were higher than those of the bacteria, indicating that fungi and bacteria were important microorganisms in litter decomposition. The fungi were dominant in the early stage of decomposition. In addition, the different response of decomposition of the *E. vaginatum* and *Sphagnum* litter to the addition of N helps to assess the effects of addition of N on C and nutrient dynamics during the vegetation succession from mosses to vascular plants in permafrost peatlands under climate change.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2021.105801.

References

Aerts, R., Wallen, B., Malmer, N., 1992. Growth-limiting nutrients in *Sphagnum* -dominated bogs subject to low and high atmospheric nitrogen supply. J. Ecol. 80, 131–140. https://doi.org/10.2307/2261070.

Aerts, R., Walle'n, B., Malmer, N., De Caluwe, H., 2001. Nutritional constraints on *Sphagnum*-growth and potential decay in northern peatlands. J. Ecol. 89, 292-299. 10.1046/j.1365-2745.2001.00539.x.

Allison, S.D., Vitousek, P.M., 2004. Extracellular enzyme activities and carbon chemistry as drivers of tropical plant litter decomposition. Biotropica 36, 285-296. 10.1111/j.1744-7429.2004.tb00321.

Bai, Z., Ma, Q., Wu, X., Zhang, Y.I.A., Yu, W.T., 2017. Temperature sensitivity of a PLFA-distinguishable microbial community differs between varying and constant temperature regimes. Geoderma 308, 54–59. https://doi.org/10.1016/j.geoderma.2017.08.026.

Bell, M.C., Ritson, J.P., Verhoef, A., Brazier, R.E., Templeton, M.R., Graham, N.J.D., Freeman, C., Clark, J.M., 2018. Sensitivity of peatland litter decomposition to changes in temperature and rainfall. Geoderma 331, 29–37. https://doi.org/10.1016/j.geoderma.2018.06.002.

Bian, H., Zheng, S., Liu, Y., Xu, L.i., Chen, Z., He, N., 2020. Changes to soil organic matter decomposition rate and its temperature sensitivity along water table gradients in cold-temperate forest swamps. Catena 194, 104684. https://doi.org/10.1016/j.catena.2020.104684.

Bragazza, L., Bardgett, R.D., Mitchell, E.A.D., Buttler, A., 2015. Linking soil microbial communities to vascular plant abundance along a climate gradient. New Phytol. 205 (3), 1175–1182. https://doi.org/10.1111/nph.13116.

Bragazza, L., Buttler, A., Habermacher, J., Brancaleoni, L., Gerdol, R., Fritze, H., Hanajík, P., Laiho, R., Johnson, D., 2012. High nitrogen deposition alters the decomposition of bog plant litter and reduces carbon accumulation. Glob Change Biol. 18 (3), 1163–1172. https://doi.org/10.1111/j.1365-2486.2011.02585.x.

Bragazza, L., Freeman, C., Jones, T., Rydin, H., Limpens, J., Fenner, N., Ellis, T., Gerdol, R., Hajek, M., Hajek, T., Iacumin, P., Kutnar, L., Tahvanainen, T., Toberman, H., 2006. Atmospheric nitrogen deposition promotes carbon loss from peat bogs. Proc. Natl. Acad. Sci. U. S. A. 103 (51), 19386–19389. https://doi.org/10.1073/pnas.0606629104.

Bragazza, L., Siffi, C., Iacumin, P., Gerdol, R., 2007. Mass loss and nutrient release during litter decay in peatland: The role of microbial adaptability to litter chemistry. Soil Biol. Biochem. 39 (1), 257–267. https://doi.org/10.1016/j.soilbio.2006.07.014.

Buttler, A., Robroek, B.J.M., Laggoun-Défarge, F., Jassey, V.E.J., Pochelon, C., Bernard, G., Delarue, F., Gogo, S., Mariotte, P., Mitchell, E.A.D., Bragazza, L., Morgan, J., 2015. Experimental warming interacts with soil moisture to discriminate

plant responses in an ombrotrophic peatland. J. Veg. Sci. 26 (5), 964–974. https://doi.org/10.1111/jvs.12296.
Bu, Z.-J., Rydin, H., Chen, X.u., 2011. Direct and interaction-mediated effects of environmental changes on peatland bryophytes. Oecologia 166 (2), 555–563. https://doi.org/10.1007/s00442-010-1880-1.
Craig, H., Antwis, R.E., Cordero, I., Ashworth, D., Robinson, C.H., Osborne, T.Z., Bardgett, R.D., Rowntree, J.K., Simpson, L.T., 2021. Nitrogen addition alters composition, diversity, and functioning of microbial communities in mangrove soils: An incubation experiment. Soil Biol. Biochem. 153, 108076. https://doi.org/10.1016/j.soilbio.2020.108076.
Conant, R.T., Ryan, M.G., Ågren, G.I., Birge, H.E., Davidson, E.A., Eliasson, P.E., Evans, S.E., Frey, S.D., Giardina, C.P., Hopkins, F.M., Hyvönen, R., Kirschbaum, M.U. F., Lavallee, J.M., Leifeld, J., Parton, W.J., Megan Steinweg, J., Wallenstein, M.D., Martin Wetterstedt, J.Å., Bradford, M.A., 2011. Temperature and soil organic matter decomposition rates – synthesis of current knowledge and away forward. Global Change Biol. 17 (11), 3392–3404. https://doi.org/10.1111/j.1365-2486.2011.02496.x.
Cornelissen, J.H.C., van Bodegom, P.M., Aerts, R., Callaghan, T.V., van Logtestijn, R.S.P., Alatalo, J., Stuart Chapin, F., Gerdol, R., Gudmundsson, J., Gwynn-Jones, D., Hartley, A.E., Hik, D.S., Hofgaard, A., Jónsdóttir, I.S., Karlsson, S., Klein, J.A., Laundre, J., Magnusson, B., Michelsen, A., Molau, U., Onipchenko, V.G., Quested, H. M., Sandvik, S.M., Schmidt, I.K., Shaver, G.R., Solheim, B., Soudzilovskaia, N.A., Stenström, A., Tolvanen, A., Totland, Ø., Wada, N., Welker, J.M., Zhao, X., 2007. Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. Ecol. Lett. 10 (7), 619–627. https://doi.org/10.1111/j.1461-0248.2007.01051.x.
Dieleman, C.M., Branfireun, B.A., McLaughlin, J.W., Lindo, Z., 2015. Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability. Global Change Biol. 21 (1), 388–395. https://doi.org/10.1111/gcb.12643.
Dorrepaal, E., Cornelissen, J.H.C., Aerts, R., Wallén, B., Van Logtestijn, R.S.P., 2005. Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? J. Ecol. 93, 817–828. https://doi.org/10.1111/j.1365-2745.2005.01024.x.
Feller, I.C., Whigham, D.F., McKee, K.L., Lovelock, C.E., 2003. Nitrogen limitation of growth and nutrient dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida. Oecologia 134 (3), 405–414. https://doi.org/10.1007/s00442-002-1117-z.
Finger, R.A., Turetsky, M.R., Kielland, K., Ruess, R.W., Mack, M.C., Euskirchen, E.S., Wurzburger, N., 2016. Effects of permafrost thaw on nitrogen availability and plant-soil interactions in a boreal Alaskan lowland. J. Ecol. 104 (6), 1542–1554. https://doi.org/10.1111/1365-2745.12639.
Hu, Z., Xu, C., Mcdowell, N.G., Johnson, D.J., Wang, M., Luo, Y., Zhou, X., Huang, Z., 2017. Linking microbial community composition to C loss rates during wood decomposition. Soil Biol. Biochem. 104, 108–116. https://doi.org/10.1016/j.soilbio.2016.10.017.
Huang, Y., Shen, Y., Zhou, M., Ma, R.S., 2003. Decomposition of plant residue as influenced by its lignin and nitrogen. Chin J Plan Ecolo 27, 183-188. (in Chinese) https://www.plant-ecology.com/CN/10.17521/cjpe.2003.0028.
Huang, X.L., Chen, J.Z., Wang, D., Deng, M.M., Wu, M.Y., Tong, B.L., Liu, J.M., 2021. Simulated atmospheric nitrogen deposition inhibited the leaf litter decomposition of *Cinnamomum migao* H. W. Li in Southwest China. Sci. Rep. 11 (1), 1748 https://doi.org/10.1038/s41598-021-81458-3.
Hugelius, G., Strauss, J., Zubrzycki, S., Harden, J.W., Schuur, E.A.G., Ping, C.-L., Schirrmeister, L., Grosse, G., Michaelson, G.J., Koven, C.D., O'Donnell, J.A., Elberling, B., Mishra, U., Camill, P., Yu, Z., Palmtag, J., Kuhry, P., 2014. Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps. Biogeosciences 11 (23), 6573–6593. https://doi.org/10.5194/bg-11-6573-2014.
Jiang, X., Cao, L., Zhang, R., Yan, L., Mao, Y., Yang, Y., 2014. Effects of nitrogen addition and litter properties on litter decomposition and enzyme activities of individual fungi. Appl. Soil Ecol. 80, 108–115. https://doi.org/10.1016/j.apsoil.2014.04.002.
Keuper, F., Dorrepaal, E., van Bodegom, P.M., van Logtestijn, R., Venhuizen, G., van Hal, J., Aerts, R., 2017. Experimentally increased nutrient availability at the permafrost thaw front selectively enhances biomass production of deep-rooting subarctic peatland species. Global Change Biol. 23 (10), 4257–4266. https://doi.org/10.1111/gcb.13804.
Keuper, F., Bodegom, P.M., Dorrepaal, E., Weedon, J.T., Hal, J., Logtestijn, R.S.P., Aerts, R., 2012. A frozen feast: thawing permafrost increases plant-available nitrogen in subarctic peatlands. Global Change Biol. 18 (6), 1998–2007. https://doi.org/10.1111/j.1365-2486.2012.02663.x.
Koerselman, W., Meuleman, A.F.M., 1996. The vegetation N: P ratio: a new tool to detect the nature of nutrient limitation. J. Appl. Ecol. 33, 1441–1450. https://doi.org/10.2307/2404783.
Lang, S.I., Cornelissen, J.H.C., Klahn, T., Van Logtestijn, R.S.P., Broekman, R., Schweikert, W., Aerts, R., 2009. An experimental comparison of chemical traits and litter decomposition rates in a diverse range of subarctic bryophyte, lichen and vascular plant species. J. Ecol. 97, 886–900. https://doi.org/10.1111/j.1365-2745.2009.01538.x.
Liu, G., Sun, J., Tian, K., Xiao, D., Yuan, X., 2017. Long-term responses of leaf litter decomposition to temperature, litter quality and litter mixing in plateau wetlands. Freshw. Biol. 62 (1), 178–190. https://doi.org/10.1111/fwb.12860.
Liu, G.M., Zhang, X.L., Wu, T.H., Wu, X.L., Smoak, J.M., Li, X.X., Ji, G.H., Xu, H.Y., Ma, X.L., Li, H.Q., Yue, G.Y., Ding, Y.J., Zhao, L., Wu, X.D., 2019. Seasonal changes in labile organic matter as a function of environmental factors in a relict permafrost region on the Qinghai-Tibetan Plateau. Catena 180, 194–202. https://doi.org/10.1016/j.catena.2019.04.026.
Liu, Y., Chen, Y., Zhang, J., Yang, W., Peng, Z., He, X., Deng, C., He, R., 2016. Changes in foliar litter decomposition of woody plants with elevation across an alpine forest–tundra ecotone in eastern Tibet Plateau. Plant Ecol. 217, 495–504. https://doi.org/10.1007/s11258-016-0594-9.
Lovelock, C.E., Feller, I.C., Mckee, K.L., Engelbrecht, B.M.J., Ball, M.C., 2004. The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panama. Funct. Ecol. 18, 25–33. https://doi.org/10.1046/j.0269-8463.2004.00805.x.
Manninen, S., Kivimäki, S., Leith, I.D., Leeson, S.R., Sheppard, L.J., 2016. Nitrogen deposition does not enhance *Sphagnum* decomposition. Sci. Total Environ. 571, 314–322. https://doi.org/10.1016/j.scitotenv.2016.07.152.
Mao, R., Zhang, X., Song, C., Wang, X., Finnegan, P.M., 2018. Plant functional group controls litter decomposition rate and its temperature sensitivity: An incubation experiment on litters from a boreal peatland in northeast China. Sci. Total Environ. 626, 678–683. https://doi.org/10.1016/j.scitotenv.2018.01.162.
Mckee, K.L., Cahoon, D.R., Feller, I.C., 2007. Caribbean mangroves adjust to rising sea level through biotic controls on change in soil elevation. Glob. Ecol. Biogeogr. 16, 545–556. https://doi.org/10.1111/j.1466-8238.2007.00317.x.
Moore, T.R., Bubier, J.L., Bledzki, L., 2007. Litter decomposition in temperate peatland ecosystems: The effect of substrate and site. Ecosystems 10, 949-963. https://link.springer.com/article/10.1007/s10021-007-9064-5.
Menéndez, M., Hernández, O., Comín, F.A., 2003. Seasonal comparisons of leaf processing rates in two Mediterranean rivers with different nutrient availability. Hydrobiologia 495, 159–169. https://doi.org/10.1023/A:1025462708460.
Nikonova, L. G., Golovatskaya, E. A., Terechshenko, N. N., 2018. Decomposition rate of peat-forming plants in the oligotrophic peatland at the first stages of destruction. IOP Conference Series: Earth and Environmental Science 138, 012013. https://iopscience.iop.org/article/10.1088/1755-1315/138/1/012013.
Nilsson, M., Bååth, E., Söderström, B., 1992. The microfungal communities of a mixed mire in northern Sweden. Can. J. Botany 70 (2), 272–276. https://doi.org/10.1139/b92-037.
Ramirez, K.S., Craine, J.M., Fierer, N., 2012. Consistent effects of nitrogen amendments on soil microbial communities and processes across biomes. Glob Change Biol 18, 1918–1927. https://doi.org/10.1111/j.1365-2486.2012.02639.x.
Robertson, G.P., Blair, J.M., Groffman, P.M., Harris, D., Holland, E., Nadelhoffer, K., Wedin, D., 1999. Soil carbon and nitrogen availability: nitrogen mineralization, nitrification, and soil respiration potentials. In: Robertson, G.P., Bledsoe, C.S., Coleman,D.C., Sollins, P. (Eds.), Standard Soil Methods for Long-term Ecological Research.Oxford University Press, New York, pp. 258-271. https://www.researchgate.net/publication/304047637_Soil_carbon_and_nitrogen_availability_nitrogen_mineralization_nitrification_and_soil_respiration_potentials.
Song, Y.Y., Song, C.C., Meng, H.N., Swarzenski, C.M., Wang, X.W., Tan, W.W., 2017. Nitrogen additions affect litter quality and soil biochemical properties in a peatland of Northeast China. Ecol. Eng. 100, 175–185. https://doi.org/10.1016/j.ecoleng.2016.12.025.
Song, Y.Y., Song, C.C., Ren, J.S., Ma, X.Y., Tan, W.W., Wang, X.W., Gao, J.L., Hou, A.X., 2019. Short-term response of the soil microbial abundances and enzyme activities to experimental warming in a boreal peatland in Northeast China. Sustainability 11 (3), 590. https://doi.org/10.3390/su11030590.
Song, Y.Y., Song, C.C., Ren, J.S., Tan, W.W., Jin, S.F., Jiang, L., 2018a. Influence of nitrogen additions on litter decomposition, nutrient dynamics, and enzymatic activity of two plant species in a peatland in Northeast China. Sci. Total Environ. 625, 640–646. https://doi.org/10.1016/j.scitotenv.2017.12.311.
Song, Y.Y., Song, C.C., Hou, A.X., Ren, J.S., Wang, X.W., Cui, Q., Wang, M.Q., 2018b. Effects of temperature and root additions on soil carbon and nitrogen mineralization in a predominantly permafrost peatland. Catena 165, 381–389. https://doi.org/10.1016/j.catena.2018.02.026.
Sundh, I., Nilsson, M., Borgå, P., 1997. Variation in microbial community structure in two boreal peatlands as determined by analysis of phospholipid fatty acid profiles. Appl. Environ. Microbiol. 63, 1476–1482. https://doi.org/10.1128/aem.63.4.1476-1482.1997.
Tao, B., Wang, Y., Yu, Y., Li, Q., Luo, C., Zhang, B., 2018. Interactive effects of nitrogen forms and temperature on soil organic carbon decomposition in the coastal wetland of the Yellow River Delta, China. Catena 165, 408–413. https://doi.org/10.1016/j.catena.2018.02.025.
Tarnocai, C., 2009. The impact of climate change on Canadian peatlands. Can. Water Resour. J. 34, 453–466. https://doi.org/10.4296/cwrj3404453.
Tarnocai, C., Canadell, J.G., Schuur, E.A.G., Kuhry, P., Mazhitova, G., Zimov, S., 2009. Soil organic carbon pools in the northern circumpolar permafrost region. Global Biogeochem. Cycles 23, GB2023. https://doi.org/10.1029/2008GB003327.
Trofymow, J.A., Moore, T.R., Titus, B., Prescott, C., Morrison, I., Siltanen, M., Smith, S., Fyles, J., Wein, R., Camiré, C., Duschene, L., Kozak, L., Kranabetter, M., Visser, S., 2002. Rates of litter decomposition over 6 years in Canadian forests: Influence of litter quality and climate. Can. J. For. Res. 32, 789–804. https://doi.org/10.1139/x01-117.
Trogisch, S., He, J., Hector, A., Scherer-Lorenzen, M., 2016. Impact of species diversity, stand age and environmental factors on leaf litter decomposition in subtropical forests in China. Plant Soil 400, 337-350. http://www.jstor.org/stable/43872589.
Turetsky, M.R., Crow, S.E., Evans, R.J., Vitt, D.H., Wieder, R.K., 2008. Trade-offs in resource allocation among moss species control decomposition in boreal peatlands. J. Ecol. 96, 1297–1305. https://doi.org/10.1111/j.1365-2745.2008.01438.x.
van Breemen, N., 1995. How *Sphagnum* bogs down other plants. Trends Ecol. Evol. 10, 270–275. https://doi.org/10.1016/0169-5347(95)90007-1.
van den Elzen, E., van den Berg, L.J.L., van der Weijden, B., Fritz, C., Sheppard, L.J., Lamers, L.P.M., 2018. Effects of airborne ammonium and nitrate pollution strongly

differ in peat bogs, but symbiotic nitrogen fixation remains unaffected. Sci. Total Environ. 610, 732–740. https://doi.org/10.1016/j.scitotenv.2017.08.102.

Wang, Z.C., Liu, S.S., Bu, Z.J., Wang, S.Z., 2018. Degradation of polycyclic aromatic hydrocarbons (PAHs) during *Sphagnum* litters decay. Environ. Sci. Pollut. Res. 25, 18642–18650. https://link.springer.com/article/10.1007/s11356-018-2019-x.

Waring, B.G., 2013. Exploring relationships between enzyme activities and leaf litter decomposition in a wet tropical forest. Soil Biol. Biochem. 64, 89–95. https://doi.org/10.1016/j.soilbio.2013.04.010.

Xing, Y., Bubier, J., Moore, T., Murphy, M., Basiliko, N., Wendel, S., Blodau, C., 2011. The fate of ^{15}N-nitrate in a northern peatland impacted by long term experimental nitrogen, phosphorus and potassium fertilization. Biogeochemistry 103, 281–296. https://doi.org/10.1007/s10533-010-9463-0.

Zhang, X.H., Sun, X.X., Mao, R., 2017. Effects of litter evenness, nitrogen enrichment and temperature on short-term litter decomposition in freshwater marshes of northeast China. Wetlands 37, 145–152. https://doi.org/10.1007/s13157-016-0855-3.

Zhang, X.H., Wang, X., Finnegan, P.M., Tan, W., Mao, R., 2019. Effects of litter mixtures on aerobic decomposition rate and its temperature sensitivity in a boreal peatland. Geoderma 354, 113890. https://doi.org/10.1016/j.geoderma.2019.113890.

Zeh, L., Igel, M.T., Schellekens, J., Limpens, J., Bragazza, L., Kalbitz, K., 2020. Vascular plants affect properties and decomposition of moss-dominated peat, particularly at elevated temperatures. Biogeosciences 17, 4797–4813. https://doi.org/10.5194/bg-17-4797-2020.

Zeng, J., Bu, Z. J., Wang, M., Ma, J. Z., Wang, S.Z., 2013. Effects of nitrogen deposition on peatland: a review. Chinese J. Ecol. 32, 473-481. (in Chinese) https://www.researchgate.net/publication/287430076_Effects_of_nitrogen_deposition_on_peatland_A_review.