Litter decomposition rates in a post-mined peatland: determining factors studied in litterbag experiments

Ryoji Nakanishi[1] • **Shiro Tsuyuzaki**[2] (ID)

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e-mail: Shiro Tsuyuzaki

tsuyu@ees.hokudai.ac.jp (ID 0000-0003-3010-8699)

[1] Graduate School of Environmental Science, Hokkaido University, Sapporo 060-0810, Japan

[2] Graduate School of Environmental Earth Science, Hokkaido University, Sapporo 060-0810, Japan

Abstract

The litter decomposition process is one of the keys to restoring wetlands after peat mining, because litter decomposition largely determines peat regeneration. We monitored the process on a post-mined peatland in northern Japan from 2020 to 2021 with litter species and the environments (surface temperature, shade and moisture). Litterbag experiments were conducted by two litter species, *Moliniopsis japonica* and *Sphagnum papillosum* because the succession was replaced from *M. japonica* grassland (MJ) to *Sphagnum* mat (SP). Three environments were developed: unshaded control, black shear net and white net. %C, %N, δ^{13}C and δ^{15}N in the litter were measured with litter mass remaining. Black nets showed lower mean temperatures with smaller variations than white nets. SP showed lower water level and peat moisture than MJ. Litter decomposition was faster in the black nets than in the white nets. These results indicated that litter decomposition was regulated by temperature fluctuation and its related factors, rather than mean temperature. *Sphagnum* showed a home-field advantage in decomposition, whereas *M. japonica* did not. δ^{13}C and δ^{15}N were lower and higher in *Sphagnum* litter than in *M. japonica* litter, respectively, showing that N and C components differed between litter species. The high δ^{15}N in *Sphagnum* litter indicated that intracellular N_2 fixers contributed to N in the litter. In conclusion, litter decomposition was not faster at higher temperatures and was determined primarily by litter species.

Article highlights

- Higher temperature did not increase litter decomposition rates in the post-mined wetlands.
- Home field advantage was dependent on litter species.
- Ecological succession should be considered to understand litter decomposition processes.

Keywords litterbag experiment · litter decomposition rate · stable isotope · litter species · home-field advantage (HFA) · peatland litter · peat-mined bog · wetland litter

1 Introduction

Although boreal peatlands represented by bogs, as a huge carbon sink, contain 1/3 of the soil organic C in terrestrial ecosystems in the world (Gorham 1991), peatlands have declined because of human activities, such as peat mining, land use change and global warming (Tsuyuzaki and Zhang 2020, Wang et al. 2022). The degradation of peatlands has recently contributed 5-10% of global annual anthropogenic CO_2 emissions (Loisel and Gallego-Sala 2022). Global climate change affects litter decomposition through changes in temperature, moisture and microbial activity (Bardgett et al. 2008, Xie et al. 2019), because litter decomposition in boreal peatlands is slow under low temperatures, anoxic conditions and functionally limited decomposer communities (Freeman et al. 2001, Moore et al. 2007). Because the amount of peat accumulation is determined by a balance between the decomposition and accumulation of litter, studies are required to understand how climate change impacts litter decomposition in peatlands (Salimi et al. 2021). However, litter decomposition proceeds with complicated and multiple interactions among climatic factors, i.e., temperature and precipitation, and decomposer composition (García-Palacios et al. 2016). Litter species also affect the decomposition (Gholz et al. 2000, Otaki and Tsuyuzaki 2019).

Litter decomposition in boreal regions is slow, due to low temperature that does not activate litter-decomposing microbes (Strakova et al. 2011). Therefore, the effects of temperature on litter decomposition should be investigated. Litterbag experiments have been widely applied to investigate litter decomposition processes (Otaki et al. 2016), although litterbags induce artifacts, such as changing temperature and shade and excluding macro-invertebrates in litterbags (Paudel et al. 2015, Prescott and Vesterdal 2021). However, temperature manipulation experiments can be performed using litterbags if we change our point of view.

Although home-field advantage (HFA), one of the major hypotheses explaining litter decomposition rates, has been examined, the intensity and mechanisms of HFA remain controversial (Fanin et al. 2021). For example, HFA is rejected in the Atlantic rainforest of Brazil (Bießelmann et al. 2011), whereas it is accepted in the deciduous temperate forests of Hokkaido, Japan (Otaki and Tsuyuzaki 2019). HFA clearly appears when standing vegetation determines the dominance of litter species (Veen et al. 2014). Across succession in wetlands, including fens and bogs, the dominant plants

73 often change from grasses to peat mosses, i.e., *Sphagnum* spp. (Laine et al. 2011). *Sphagnum*-peat
74 mining had been conducted in Sarobetsu mire, northern Japan, from 1970 to 2003 for commercial use
75 (Nishimura et al. 2009). *Sphagnum* in the mined sites did not return to the original vegetation in various
76 locations even 40 years after mining. Therefore, active restoration is required to promote the recovery
77 of bogs that support high biodiversity by serving as habitats for endangered and rare species (Limpens
78 et al. 2011). Since the vegetation changes from *M. japonica* grassland to *Sphagnum* mat in the post-
79 mined peatland across the succession (Nishimura and Tsuyuzaki 2014) and the litter composition is
80 changed with dominance of the respective species (Takeuchi et al. 2023), changes in HFA intensity
81 may be detected between litter species and between habitats across the succession when the litter of
82 *M. japonica* and *Sphagnum* were used.
83 Therefore, litterbag experiments were conducted to evaluate how litter decomposition responded
84 to changes in successional habitats and their environments in the post-mined peatlands. Three
85 hypotheses were established: 1) litter decomposition rates changed with succession from *M. japonica*
86 grassland to *Sphagnum* mat, 2) litter decomposition rates were associated with litter species, even
87 though the rates did not differ among the litter species, because of differences in chemical components
88 among the litter species, and 3) HFA functioned for late successional species more than for early
89 successional species, because of persistence, which provides predictable and stable habitats for litter-
90 decomposing microbial communities. Therefore, *Sphagnum* litter, a later colonizer, was expected to
91 show HFA more clearly than the earlier colonizer, *M. japonica*.
92

93 # 2 Study Area and Methods

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95 ## 2.1 Study Sites

96

97 Litterbag experiments were conducted in Sarobetsu mire, northern Hokkaido, Japan (45°06'N,
98 141°42'E, 7 m a.s.l.) in 2020 and 2021. The mean annual temperature was 6.3℃ for the last 30 years
99 between 1991 and 2020 with -6.1℃ at the minimum in January and 19.4℃ at the maximum in July
100 (45°06'N, 141°46'E, 16 m a.s.l., Toyotomi Town 6 km far from the study site) (JMA 2022). The mean
101 annual temperature was 6.7℃ in 2020 and 7.1℃ in 2021. The maximum monthly temperatures were

19.3℃ in August 2020 and 21.6℃ in July 2021 and the minimum temperatures lowered to -5.9℃ in February 2020 and -7.7℃ in January 2021. The annual precipitation was 1148 mm and 938 mm in 2020 and 2021, respectively. The snow-free season is usually from April to November while frost occurs sometimes in the late spring or early summer (Koyama and Tsuyuzaki 2010). The mean annual temperature raised approximately 3℃ for the last 120 years from 1900 to 2021. Annual precipitation averaged 1031 mm for the recent 30 years.

Sphagnum peat was mined annually at a rate of 3–22 ha/yr down to 3 m to 6 m, by a large dredger. The study site was mined in 1972. Soon after peat mining, open water developed broadly. Thereafter, the peat residues floated and developed bareground. Habitats along the successional sere are ordered from early to late stages as bare ground (hereafter, i.e., BG), *Rhyncospora alba* grassland (RA), *Moliniopsis japonica* grassland (MJ) and *Sphagnum* mat (SP) (Nishimura et al. 2009). In 2019, vegetation data were obtained from BG, RA, MJ and SP, by using 15 50 cm × 50 cm plots in each habitat. The total plant cover, including mosses, averaged 2% in BG, 76% in RA, 199% in MJ and 162% in SP. BG accumulated the least litter and RA did less. Total plant cover is the sum of the area covered by each plant species. Therefore, MJ and SP were used for the litter decomposition experiments. In 2020 and 2021, the vegetation was monitored in these plots on MJ and SP.

2.2 Litterbag Experiments

Nine 1 m × 1 m plots were established in each of the SP and MJ in August 2020. In mid-October 2020, the litter of *M. japonica* leaves and *Sphagnum papillosum* shoots were collected adjacent to the plots and kept in plastic bags. Litter produced in 2020 was collected based on visual estimation. These litter samples were immediately carried to the lab and dried at a mild temperature, 60℃, for 5 days (Osborne et al. 2021).

Litterbags (10 cm × 9 cm) were made by polyethylene shear nets with 1-mm mesh and were filled with 1.4 g of dry weight of either *S. papillosum* or *M. japonica* litter. Black and white litterbags were prepared with shear nets (mesh size = 1 mm × 1 mm) to provide different temperatures and light intensities in the bags (Dio Chemicals Co. Ltd., Tokyo, Japan). Although litterbags with 1-2 mm mesh are the most common, the mesh size should be larger than 2 mm when considering macrofauna

131 (Karberg et al. 2008). However, macrofauna are not abundant in the post-mined peatland (Tsuyuzaki
132 et al. 2022). A total of 230 litterbags were set up in each of the MJ and SP on 15 November 2020. Four
133 litterbags were recovered from each plot on May 30, August 13 and October 24 in 2021. The recovered
134 litterbags were dried at 60℃ for 5 days and re-weighed.

135 The litter samples were homogenized by an electric grinder. The content of nitrogen (%N) and
136 carbon (%C) was measured by an isotope mass spectrometer (Finnigan MAT252, Thermo Fisher
137 Scientific, Yokohama, Japan). δ^{15}N (‰) and δ^{13}C (‰) were measured concurrently with %N and %C.
138 δ^{15}N and δ^{13}C were calculated as $(R_{sample} / R_{standard} - 1) \times 1000$, where R_{sample} was $^{15}N/^{14}N$ or $^{13}C/^{12}C$
139 and $R_{standard}$ was the reference, atmospheric N for δ^{15}N and Vienna Peedee Belemnite (VPDB) for δ^{13}C
140 (Coetsee et al. 2010). Based on the %C and %N, the C/N ratio was calculated, as this ratio often
141 decreases with proceeding litter decomposition (Otaki and Tsuyuzaki 2019). δ^{15}N and δ^{13}C can be used
142 to elucidate processes that mediate various ecosystem functions (Kostka et al. 2016, Kwon and
143 Tsuyuzaki 2016).
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145 **2.3 Measurements of Environmental Factors**

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147 The temperature and light intensity were measured at 1-hour intervals from 19 June 2020 to 23 October
148 2021 by automatic data loggers (HOBO Temperature/Light Data Logger, Onset Computer Corporation,
149 Cape Cod, USA) placed on plots in MJ and SP. Three loggers were installed on each habitat. The first
150 one was unshaded control, the second one was shaded by a white shear net and the third one is shaded
151 by a black net. The ground-surface temperature on BG was additionally monitored on May 29 and
152 October 23 in 2021. Peat moisture (v/v) was measured at 1-hr intervals by a time domain reflectometer
153 (EC-5 ECH2O, Decagon Devices, Pullman, WA, USA) installed at 5 cm deep in each of MJ and SP
154 on June 20 and October 22 in 2021.

155 Groundwater level was measured by PVC pipes (1 m in length and 4 cm in diameter with holes
156 at 20 cm intervals) installed into each of the four habitats, BG, RA, MJ and SP, in May 2021. The water
157 level was measured during the snow-free seasons in 2021 and 2022. In this study, a negative value
158 shows that the groundwater surface is below the ground surface, and *vice versa*. pH in surface water
159 was measured by a pH meter (HI981030, Hanna Instruments Japan Co. Ltd., Chiba, Japan) and was

used after calibration. Dissolved oxygen (DO) and temperature in surface water were measured by a DO meter (WTW-W2FD350, Xylem Analytics, Weilheim, Germany) in each of the four habitats. DO and temperature in surface water were measured on May 30, August 28 and October 24, 2021. pH was also measured on August 13, 2021. On each environmental factor, the replications were three in each habitat on each census.

2. 4 Statistical Analysis

The litter remaining mass was calculated as $y_t/y_0 \times 100$ %, where y_0 is the initial litter mass and y_t is the remaining mass at time t. The litter decomposition rate (k, day^{-1}) was obtained by the duration and litter remaining mass, as $y/y_0 = e^{-kt}$ (Makkonen et al. 2012).

The five chemical parameters, %N, %C, δ^{15}N, δ^{13}C and C/N ratio, in the initial litter were compared between *M. japonica* and *S. papillosum* by GLM with the assumption of gaussian distribution. As well, k and the five parameters in the litter collected from the field were compared among litter species, habitats, shear nets and periods by GLMs with gaussian distribution and identity link (Dobson and Barnett 2018). The interactions between litter species and habitats were inserted into the GLMs to detect HFA. Akaike's Information Criteria (AIC) were used to obtain the fittest models to explain the process of changes in litter mass remaining (Venables and Ripley 2002). The AIC was not used in the other GLMs. Water level, pH, water temperature and peat moisture were compared between the habitats by a generalized linear mixed-effects model (GLMM) with the assumption of gaussian distribution and the random effect of sampling date (Bates et al. 2015).

The daily mean, maximum and minimum temperatures were calculated. Temperature fluctuation was expressed by the standard deviation of temperature each day. The maximum and minimum temperatures in a day were compared by GLMM between the habitats and between the nets with their interactions and period as a random effect. All analyses were conducted using R ver. 4.1.1 (R Development Core Team 2022). For specific analyses, the following R libraries were used: MASS (Venables and Ripley 2002), lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2017) and vegan (Oksanen et al. 2022).

3 Results

3.1 Litter Decomposition

In the initial litter, when the samples were collected, the %C in litter was higher in *M. japonica* than in *Sphagnum* (GLM, $p < 0.001$) (Table 1). %N and C/N ratio did not differ between the two litter species ($p = 0.069$ and $p = 0.483$, respectively). *M. japonica* litter showed higher δ^{13}C than *Sphagnum* litter ($p < 0.001$). A large difference in δ^{15}N was detected between the two litter species, -4.90 in *M. japonica* and -2.85 in *Sphagnum* ($p = 0.016$).

The litter mass remaining was 70-80% in late October 2021, one year after the litterbags were set up (Fig. 1). The litter species and habitats were not adopted in the fittest GLM selected by AIC, indicating that the litter species and habitats affected less the decomposition. However, the interactions between the species and habitats were adopted in the model. By contrast, litter remained in white nets more than in black nets.

Litter decomposition coefficients (k) ranged from 0.14 to 0.46 (Table 2). As well as the litter mass remaining, k differed neither between the litter species nor between the habitats (GLM, $p > 0.652$). The litter in black shear nets showed higher k than the litter in white nets (slope = -0.0257, $p < 0.001$), showing that the black nets promoted faster litter decomposition. The k increased with increasing periods (+0.0002, $p = 0.002$), indicating that the litter decomposition became faster with increasing time. This trend appeared clearly in the *M. japonica* litter but did not do on the *Sphagnum* litter. The interaction was detected between the habitats, *Sphagnum* litter and *Sphagnum* mat (+0.085, $p < 0.001$), showing that *Sphagnum* litter decomposed faster on SP than on MJ. This interaction was observed even when the effects of black and white litterbags were examined separately.

From spring to fall in 2021, excluded the initial litter, both %C and N% increased (GLM, $p < 0.001$) (Fig. 2). *Sphagnum* litter showed lower %C and higher %N than *M. japonica* litter throughout the surveyed period (GLM, $p < 0.001$). %C was lower in SP ($p < 0.001$). On %N, the interaction was detected between litter species and habitats ($p < 0.001$). The nets were discarded from the fittest model by AIC, showing that the differences in nets were not related to %C, while the black nets increased %N more than white nets ($p < 0.001$). To explain temporal changes in δ^{13}C, the period was not adopted in

the fittest model (Fig. 3). $\delta^{13}C$ was higher in *M. japonica* litter than *Sphagnum* litter throughout the surveyed period, as well as the initial litter. The habitats remained in the model of $\delta^{13}C$, although the effect was not significant ($p = 0.129$). In contrast, $\delta^{15}N$ increased with time ($p < 0.001$). Neither $\delta^{13}C$ nor $\delta^{15}N$ differed between the nets. These results meant that %N in the litter was altered through the decomposition processes more than %C.

3.2 Vegetation and the Environments

In total, 16 vascular plant species were recorded (Table 3). Of non-vascular plants, *Sphagnum papillosum* was predominant. Species richness and plant cover, including mosses, per plot ranged from 4 to 10 and from 81% to 213%, respectively. The richness and total plant cover were not different between habitats (GLMM, $p > 0.05$) and between years ($p > 0.05$), while the total vascular plant cover was higher ($p = 0.007$) in MJ independent of the years ($p = 0.073$). On all the vegetation analyses, their interactions were not significant ($p > 0.05$). The dominant species were *M. japonica* (60% on average) and *Carex middendorffii* (23-37%) in MJ and *Sphagnum* mosses (75-81%) and *M. japonica* (23-37%) in SP. As *Sphagnum* cover was 4-6% in MJ and 75-81% in SP, the ground surface was covered with thick *M. japonica* litter in MJ and with *Sphagnum* litter in SP. Therefore, the ground surface was physically and/or topographically different between MJ and SP. The heights of *M. japonica* averaged 41 cm in MJ and 29 cm in SP.

Water level averaged -11.1 cm (range: -38.0 cm to 1.6 cm) during snowmelt periods in 2021 and 2022 (Fig. 4). The water level was higher in MJ than in SP (GLMM, $p < 0.001$), showing that the groundwater lay down in deeper peat. The water level did not differ from SP to BG and RA (non-significant at $p > 0.328$). Peat moisture ranged from 52.1% to 62.1%. The peat moisture fluctuated with the water level, i.e., decreased from June to August and increased from September to October. The peat moisture was higher in MJ than in SP ($p < 0.01$). The water level and peat moisture indicated that the water content on the ground surface tended to be higher in MJ. pH ranged between 3.27 and 5.12 from all four habitats and was not different among them (GLMM, $p > 0.089$). DO fluctuated highly between 0.29 mg/L to 9.61 mg/L and did not differ among the habitats ($p = 0.02$) when the significance level was adjusted at $p < 0.01$. The surface water temperature was 13-15ºC in spring (May),

over 25ºC in summer and 8-13ºC in autumn. The surface-water temperature was higher in BG than that in MJ ($p < 0.001$) and was not different between BG and RA and between BG and SP ($p > 0.096$).

3.3 Effects of Litterbags on Temperature and Light Intensity

The daily mean temperatures under the unshaded control were 12.4ºC ± 9.6 (range: -1.6 to 29.8) on MJ and 11.8ºC ± 9.1 (-0.7 to 28.8) on SP (Fig. 5). During May and October in 2021, the mean temperature was 0.5 ºC higher on BG than on MJ and 1.6ºC higher on BG than on SP. The black nets changed the daily temperatures at 12.1ºC ± 8.7 (-0.5 to 27.2) on MJ and at 11.7ºC ± 8.4 (0.1 to 25.9) on SP. The white nets did these at 12.5 ºC ± 9.6 (-1.6 to 30.9) on MJ and at 11.9ºC ± 8.9 (0.0 to 27.8) on SP. The black nets reduced the mean temperature (GLMM, slope = -0.376, P < 0.001), while the white nets did not change the temperature from the unshaded control ($p = 0.157$).

The temperature fluctuations were reduced greatly by the black nets (GLMM, slope = -1.46, $p < 0.01$) and weakly by the white nets (slope = -0.50, $p < 0.01$) from the unshaded control. These indicated that stresses derived by temperature fluctuations were moderated more by black nets than by white nets. The interactions between habitats and nets were significant ($p < 0.001$), showing that SP declined the temperature fluctuations more than MJ. The minimum and maximum temperatures were, respectively, higher and lower on SP than on MJ (GLMM, $p < 0.001$). The black nets increased and decreased the minimum and maximum temperatures up and down to 1.1ºC and 3.3ºC ($p < 0.01$), respectively, while the white nets increased and decreased by 0.6ºC and 1.1ºC, respectively. Therefore, the reduction of temperature fluctuations was two to three-fold higher in the black nets than in the white nets. The interaction between the habitats and nets was significant ($p < 0.01$).

The maxima of daily cumulative light intensity on the unshaded control without shear nets were 1643.0 klux on MJ and 1361.6 klux on SP. The minima were 0 in both MJ and SP recorded in winter, showing that the snow cover completely intercepted solar radiation. The cumulative light intensity without shade averaged 346.9 klux on MJ and 323.5 klux on SP. Therefore, the shade provided by the standing vegetation was primarily different between MJ and SP, i.e., the shade was more intense on SP. The cumulative light intensity was reduced by both shear nets but was not different between the habitats (GLMM, $p > 0.05$). The light intensity under white nets averaged 217.5 klux on MJ and 79.4

klux on SP, while the light intensity under the black nets was 152.9 klux on MJ and 52.3 klux on SP. The interactions between habitats and nets showed that shade was more intense in SP ($p < 0.001$). The slopes of light intensity on GLMM were -130 on the white nets and -194 on the black nets, showing that the shade was more intensive by the black nets than by the white nets (GLMM, $p < 0.001$). Because the loggers were covered somehow with growing *Sphagnum* moss on SP, the light intensity became low in the summer of 2021.

4 Discussion

4.1 Litter decomposition rates

The decomposition of litter, even for the two examined species, was faster in the black nets, which had lower mean temperatures than the white nets across the succession. High temperatures do not always increase microbial activity in the northern boreal wetlands of Finland (Peltoniemi et al. 2015). While shade (a decrease in light intensity) occurred in the black nets, along with a decrease in the mean and fluctuation of temperatures, shade had already occurred under high plant cover on MJ and SP. Light intensity determines photodegradation, which is one of the major processes of litter decomposition (Austin and Vivanco 2006), particularly in (semi-)arid ecosystems where direct sunlight is intense but bacterial activity is limited due to dry conditions (Pancotto et al. 2005). In post-mined peatlands, dryness occurs when the ground surface is not covered by plants (Girard et al. 2002, Koyama and Tsuyuzaki 2013). However, photodegradation was weakened by the shade provided by the standing vegetation in MJ and SP where the total plant cover exceeded 100%. Although shade was derived not only from the standing vegetation but also from the shear nets, the intense shade provided by the standing vegetation overshadowed the shade effects of the nets. Therefore, the shear nets should affect litter decomposition through temperature, rather than light intensity.

The microbial communities differed between MJ and SP (Tsuyuzaki et al. 2022, Takeuchi et al. 2023). These microbial communities, consisting of fungi and bacteria, are affected by climate change, particularly by precipitation, which affects the optimal temperature for litter decomposition (Glassman et al. 2018). These results suggest that the decline in temperature caused by black nets does not always

induce slow litter decomposition, and that the optimal temperature for decomposition is not high. Furthermore, the black nets significantly decreased temperature fluctuations. Large environmental fluctuations, including temperature, can impose significant stress on microbial organisms (Nguyen et al. 2021). Microbial organisms are the most active in the temperature range of 5-15ºC in European Russia (Kravchenko et al. 2019). By reducing the stress in the black nets, litter decomposition is likely to occur at a faster rate.

4.2 Litter Species and Litter Decomposition

%C in the litter was lower in the moss than in grass and on SP than on MJ, showing that %C became low when the moss was dominant. Carbon dynamics in wetlands are often affected more by litter species than by the fluctuations of peat water that determine the activities of C-acquiring enzymes in aerobic decomposers (Strakova et al. 2011).

%N and C/N ratio did not differ in the initial litter between the grass and moss. δ^{15}N was higher in *Sphagnum* litter, suggesting that the pathways and/or products of the nitrogen components differed between *M. japonica* and *S. papillosum*. However, the resulting %N was equal for grass and moss. A symbiotic relationship between *Sphagnum* mosses and cyanobacteria has been confirmed through microscopic and molecular observations (Kostka et al. 2016). The N acquisition of *Sphagnum riparium* largely depends on N_2 fixed by cyanobacteria in the moss cells (Berg et al. 2013). However, the activities of cyanobacteria, which are influenced by peat moisture, vary among *Sphagnum* species (Leppaenen et al. 2015). *Sphagnum* mosses produce specific litter, derived from low N concentrations compared to vascular plants (Dorrepaal et al. 2005). In vascular plants, N is utilized to produce persistent, structural, lignin-like, and soluble phenolic compounds (Lang et al. 2009). The litter of *Rhynchospora alba* (L.) Vahl. (Cyperaceae) does not show HFA as effective as *M. japonica*, likely because of similar litter chemistry, despite the contrasting leaf morphology between these two monocotyledonous species (Takeuchi et al. 2023). These differences are likely related to litter decomposition patterns, including temperature response and HFA.

4.3 Determinants on Litter Decomposition in Post-Mined Peatland

The litter decomposition coefficients (*k*) were higher in the presence of interactions between litter species (*Sphagnum* litter) and habitat (SP), although litter mass remaining did not differ between litter species. Namely, the decomposition rate of *Sphagnum* litter was faster in SP than in MJ and that of grass litter did not differ between SP and MJ, showing that HFA worked only for *Sphagnum* litter and that the decomposition of *M. japonica* litter did not accelerate in MJ. Fern litter decomposes faster with HFA than pine litter lacking HFA in a wide range of north and central America, probably because of differences in litter quality (Gholz et al. 2000). HFA is sometimes present when litter-decomposing fungi are host specific (Osono et al. 2021). On a post-mined peatland in Sarobetsu mire, the abundance of fungi increases along the successional sere more than the abundance of bacteria (Takeuchi et al. 2023). These suggests that interactions between plant litter and fungi are more than those between plant litter and bacteria. HFA is not detected in the Atlantic rainforest of Brazil, probably because of the composition of the litter, which consists of multiple species (Gießelmann et al. 2011). The dissimilarity in plant communities and litter quality between the home and distant locations is a major factor in promoting HFA (Veen et al. 2014). Furthermore, SP showed a lower water level and peat moisture than MJ, suggesting that the ground surface was drier on SP than on MJ. Temperature and moisture interactively affect litter decomposition in the context of climate change (Peltoniemi et al. 2015), as these factors co-vary. When peat becomes dry, litter decomposition slows due to a reduction in microbial activity (Aerts 2006, Allison and Treseder 2008). However, extremely high soil moisture induces oxygen shortages decreasing litter decomposition when precipitation is excessively high, such as in wet Hawaiian montane forests (Schuur 2001). The decomposition of *Sphagnum* litter was faster in SP, where *Sphagnum* was dominant and peat moisture was low. These suggestions indicate that litter species and the resulting HFA prevent peat from becoming too wet or dry, which affects litter decomposition. Stresses derived from DO should occur for microbes in litter, although the fluctuations in DO did not differ among the habitats.

In conclusion, temperature affected the litter decomposition rates. Furthermore, the temperature had optimal for litter decomposition, suggesting that global warming does not necessarily accelerate litter decomposition in boreal wetlands. N components in *Sphagnum* litter seem to be important for determining the decomposition dynamics. HFA functioned only for *Sphagnum* litter even in black nets

363 that altered the temperature and other environments more, suggesting that HFA had an important role
364 in litter decomposition for *Sphagnum* litter. These findings suggest that the litter decomposition is
365 altered by the supply of *Sphagnum* litter more than by *M. japonica* litter.
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378

379 ## Declarations

380 **Conflict of interest** No conflict of interest is available.
381 **Research involving human participants and animals** This study did not involve human
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383 **Informed consent** Not applicable.
384

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583 **Table 1** The chemical properties (%C, %N, C/N ratios, $\delta^{13}C$ and $\delta^{15}N$) in the initial litter of
584 *Moliniopsis japonica* and *Sphagnum papillosum*. Each numeral indicates the mean with standard
585 deviation. Probability and estimate (slope) on GLM are indicated in the right column. All the intercepts
586 on GLM are significant at $p < 0.0001$. The estimate is investigated from *M. japonica* to *S. papillosum*.
587

Litter species	*Moliniopsis japonica*	*Sphagnum papillosum*	Probability	Estimate
%C	47.4% ± 0.43	44.5% ± 0.34	< 0.001	-2.891
%N	0.83% ± 0.03	0.76% ± 0.04	0.069	-0.068
C/N ratio	57.4 ± 1.6	58.8 ± 2.7	0.483	+1.402
$\delta^{13}C$	-25.7‰ ± 0.1	-27.3‰ ± 0.2	< 0.001	-1.629
$\delta^{15}N$	-4.90 ± 0.07	-2.85 ± 0.88	0.016	+2.057

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590 **Table 2** The decomposition coefficients (*k*) of *Moliniopsis japonica* and *Sphagnum* litter in *M.*
591 *japonica* grassland and *Sphagnum* mat within black or white shear-net litterbags in 2021. The litterbags
592 were established on November 15, 2020. Each numeral shows the mean with standard deviation.
593 Significant differences are obtained between shear nets (-0.0257, $p < 0.0001$) and between periods (+
594 0.0002, $p = 0.002$) with interactions between litter species and habitats (*Sphagnum* litter × *Sphagnum*
595 mat, slope = +0.0849, $p < 0.0001$).
596

Litter species	Habitat	Litterbag	Period		
			May 30	August 13	October 24
M. japonica	*M. japonica* grassland	Black	0.200 ± 0.038	0.204 ± 0.031	0.282 ± 0.044
		White	0.192 ± 0.031	0.182 ± 0.028	0.221 ± 0.031
	Sphagnum mat	Black	0.175 ± 0.013	0.210 ± 0.020	0.216 ± 0.027
		White	0.150 ± 0.011	0.207 ± 0.030	0.269 ± 0.031
S. papillosum	*M. japonica* grassland	Black	0.261 ± 0.024	0.222 ± 0.046	0.216 ± 0.049
		White	0.212 ± 0.048	0.195 ± 0.041	0.201 ± 0.042
	Sphagnum mat	Black	0.300 ± 0.031	0.304 ± 0.039	0.308 ± 0.035
		White	0.276 ± 0.038	0.273 ± 0.062	0.288 ± 0.041

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599 **Table 3** Mean cover (%) of each species in *Moliniopsis japonica* grassland (MJ) and *Sphagnum* mat (SP) in 2020
600 and 2021. Nine 1 m× 1 m plots were established in each habitat. Mean richness and cover are shown with standard
601 deviation. -: not recorded. The occurrence frequencies are shown in parentheses. Differences in species richness, total
602 cover and total vascular plant cover are compared between habitats and between years with their interactions by
603 GLMM (Statistical results are described in the text).
604

Year	2020		2021	
Habitat	MJ	SP	MJ	SP
Moliniopsis japonica (Hack.) Hayata	60.0 (9)	22.6 (9)	60.0 (9)	37.1 (9)
Lobelia sessilifolia Lamb.	14.3 (9)	7.0 (9)	15.0 (9)	8.2 (8)
Vaccinium oxycoccos L.	10.4 (5)	4.0 (9)	8.4 (6)	4.6 (9)
Rhynchospora alba (L.) Vahl.	10.0 (8)	6.2 (6)	6.8 (8)	3.2 (7)
Carex middendorffii Fr. Schmidt	19.3 (6)	5.6 (4)	32.2 (9)	15.2 (8)
Drosera rotundifolia L.	0.1 (1)	0.6 (6)	0.4 (7)	1.3 (9)
Phragmites australis (Cav.) Trin. ex Steud.	10.2 (2)	4.4 (8)	10.2 (4)	2.7 (6)
Andromeda polifolia L.	-	1.1 (4)	-	2.2 (3)
Empetrum nigrum L.var. *japonicum* K. Koch	-	3.6 (3)	-	4.7 (3)
Eriophorum vaginatum L.	-	0.9 (2)	0.4 (2)	1.3 (1)
Sphagnum spp. (mostly *S. papillosum* Lindb.)	3.9 (6)	75.2 (9)	6.1 (7)	81.4 (9)
Species richness (/plot)	5.3 ± 0.7	8.1 ± 1.1	6.9 ± 1.1	8.6 ± 1.0
Total cover (%)	114 ± 20	144 ± 16	130 ± 17	174 ± 27
Total vascular plant cover (%)	110 ± 18	69 ± 15	124 ± 15	92 ± 20

605 * others (shown with habitats and frequencies): *Solidago virgaurea* L.ssp. *leiocarpa* (Benth.) Hultén (1 on MJ in
606 2020, 1 on SP in 2020 and 1 on MJ in 2021), *Platanthera tipuloides* (L. f.) Lindl. ssp. *nipponica* (Makino) Murata (2
607 on SP in 2021), *Scheuchzeria palustris* L. (2 on SP in 2020), *Gentiana triflora* Pall. f. *horomuiensis* (Kudo) Toyok.
608 (1 and 1 on MJ and SP, respectively, in 2020), *Myrica gale* L. var. *tomentosa* C. DC. (2 on SP in 2021), *Trientalis*
609 *europaea* L. var. *arctica* (Fisch. ex Hook.) Ledeb. (1 on SP in 2020).

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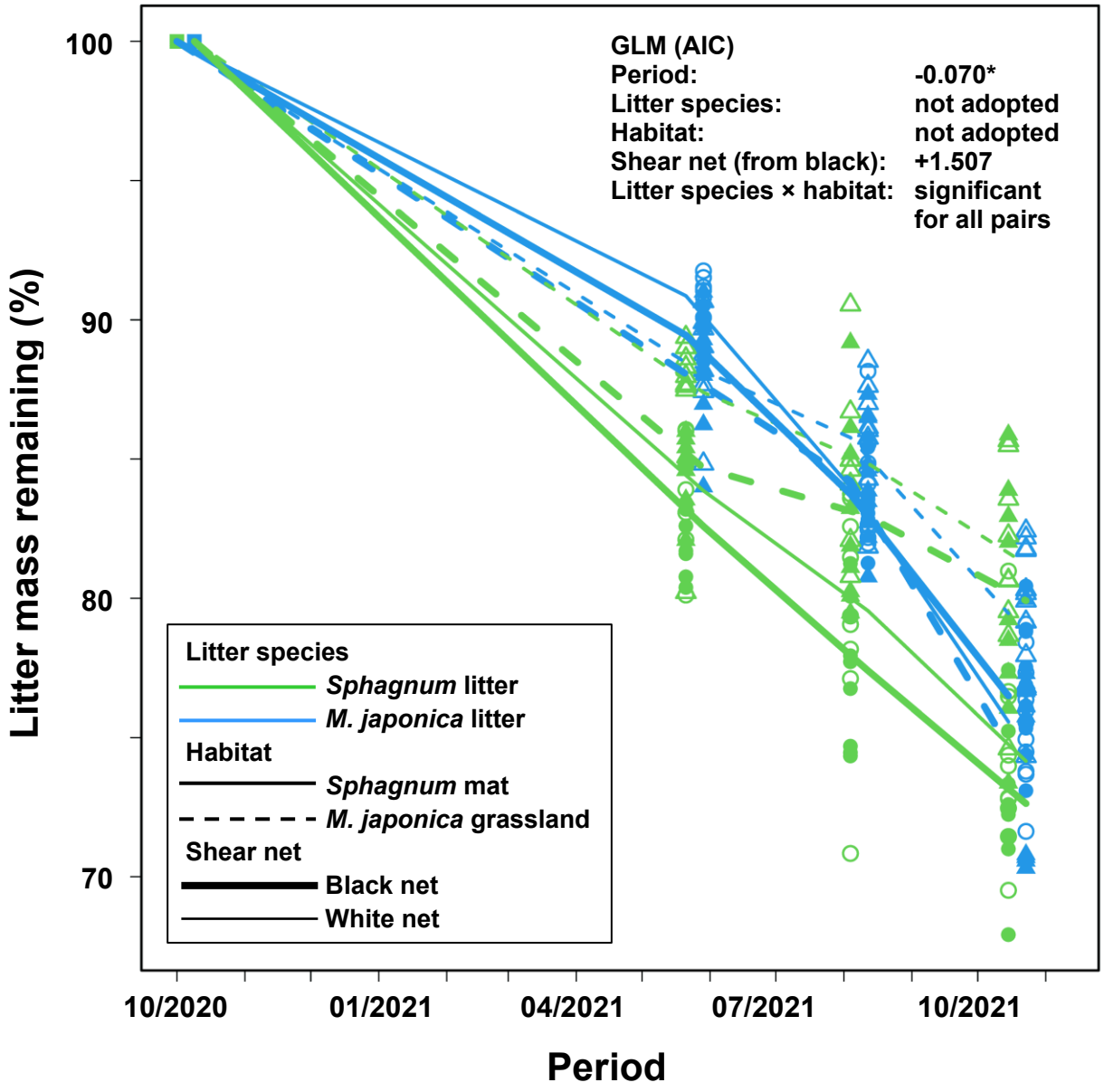


Fig 1 The temporal changes of mass remaining (%) in *Sphagnum* (green symbols and lines) and *Moliniopsis* (blue symbols and lines) litter on *Moliniopsis japonica* grassland (triangles and interrupted lines) and *Sphagnum* mat (circles and solid lines) with black (closed symbols and thick lines) and white (open symbols and thin lines) shear nets. The differences in mass remaining are compared between periods, between litter species, between habitats, and between shear nets with interactions between shear nets (GLM selected by AIC, $p < 0.01$). Numerals on the GLM indicate the slopes when the relationships are significant.

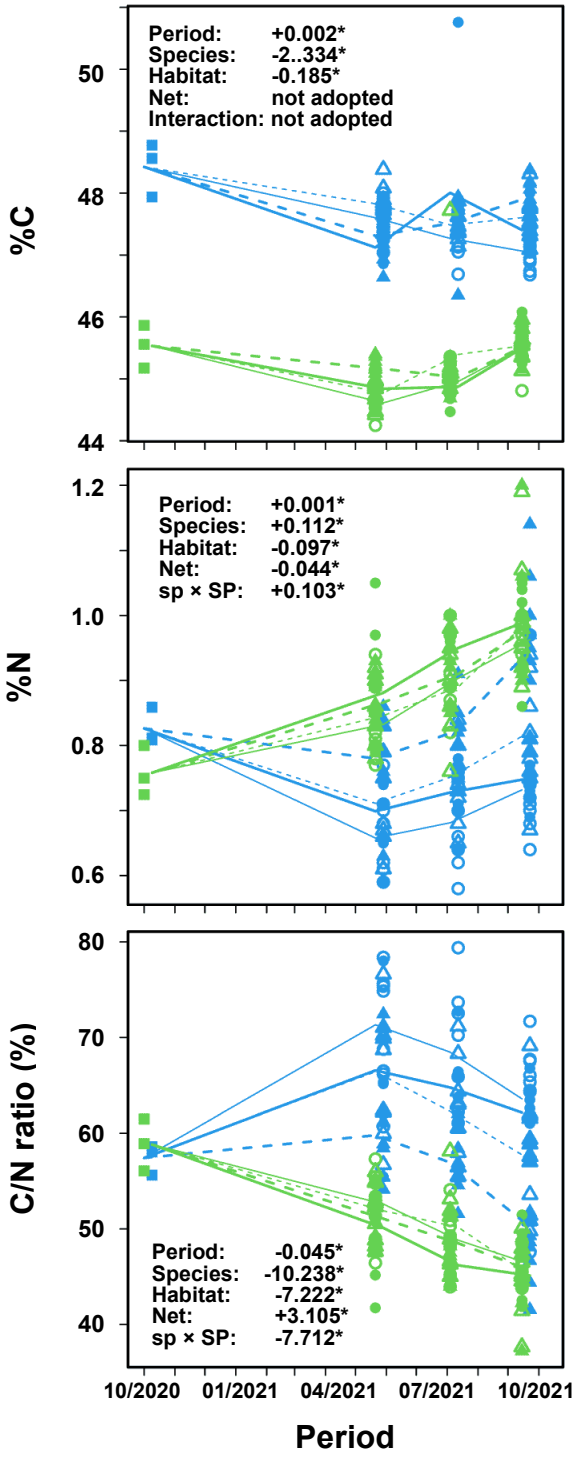
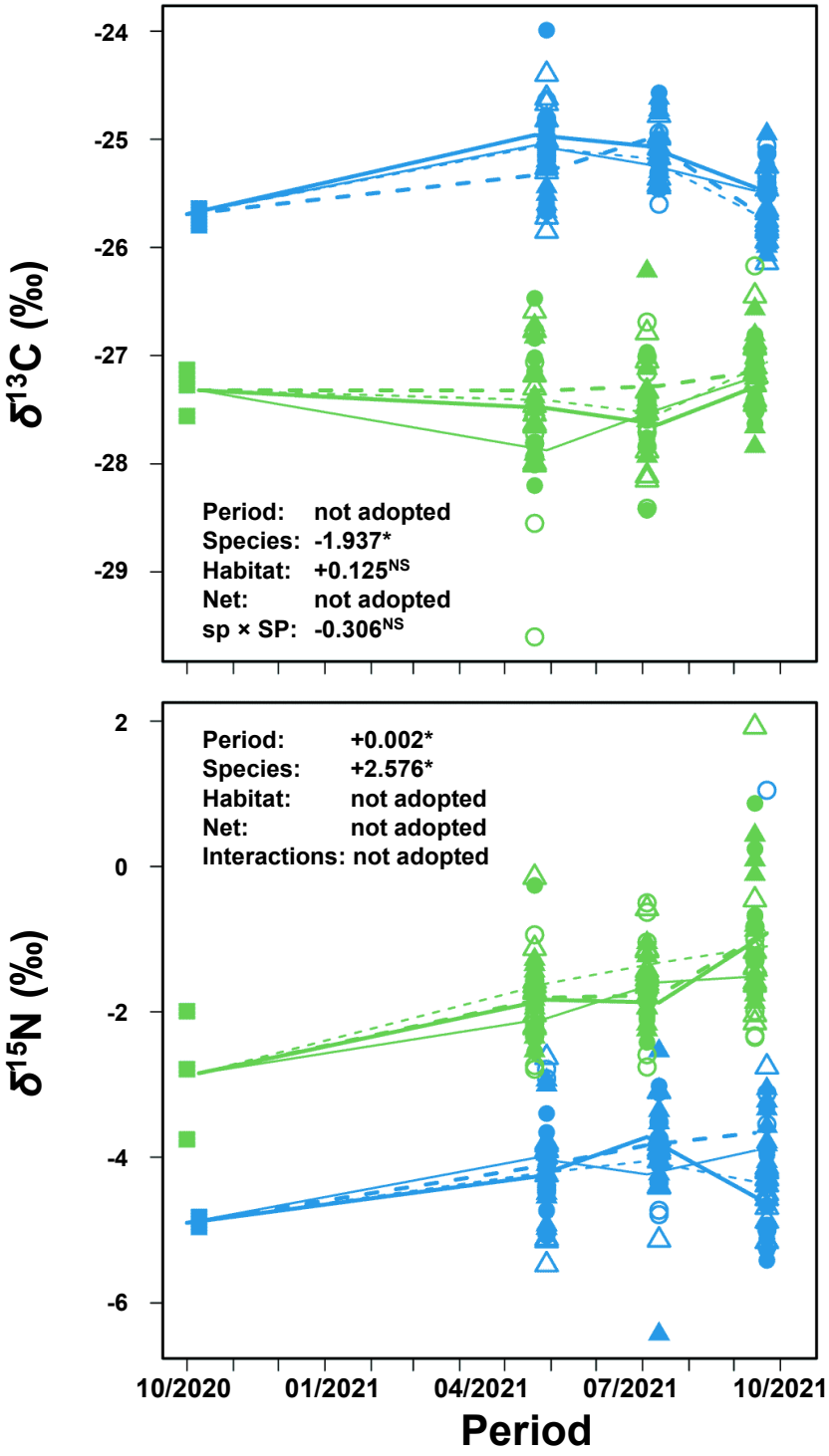


Fig 2 The temporal changes of %C, %N and C/N ratio in *Sphagnum* (green symbols and lines) and *Moliniopsis* (blue symbols and lines) litter on *Moliniopsis japonica* grassland (triangles) and *Sphagnum* mat (circles) with black (closed symbols) and white (open symbols) shear nets. The response variables are %C, %N and C/N ratio. The explanatory variables are the same with the analysis of litter mass remaining (see also Fig. 1).



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635 **Fig. 3** The temporal changes of δ^{13}C and δ^{15}N in *Sphagnum* (green symbols and lines) and *Moliniopsis*
636 (blue symbols and lines) litter on *Moliniopsis japonica* grassland (triangles) and *Sphagnum* mat
637 (circles) with black (closed symbols) and white (open symbols) shear nets. GLMs are conducted to
638 investigate the differences. The response variables are δ^{13}C and δ^{15}N and the explanatory variables are
639 the same with the analysis of litter mass remaining (see also Fig. 1).
640

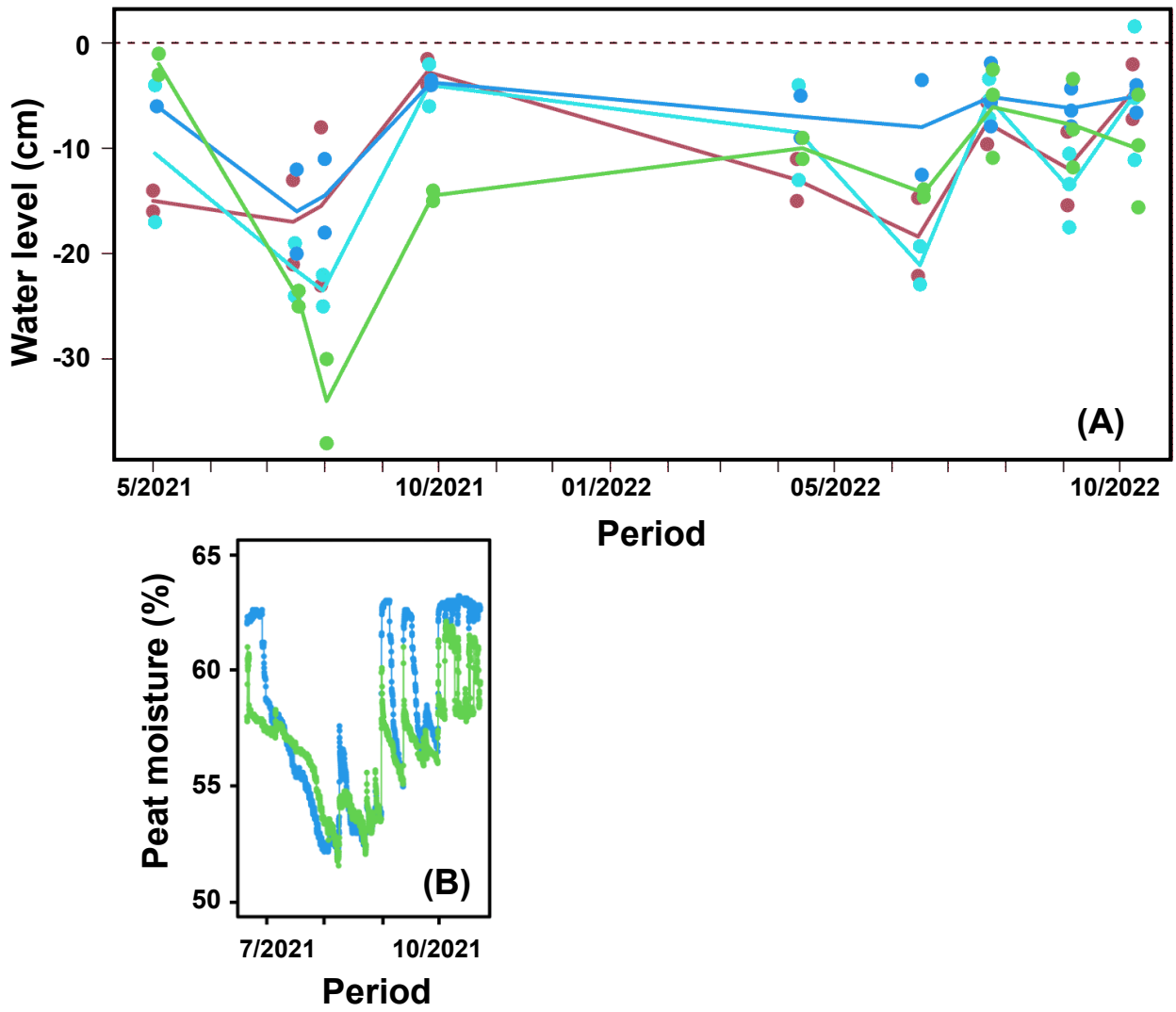

Fig. 4 The temporal fluctuations of water level in the four habitats in 2021 and 2022 (A) and peat moisture in *M. japonica* grassland and *Sphagnum* mat in 2021 (B) during the snow-melting periods. Habitat: red = bareground, cyan = *R. alba* grassland, blue = *M. japonica* grassland and green = *Sphagnum* mat. Interrupted line shows that the water level is zero. The water level is lower in SP than in MJ (GLMM, slope = -5.283, $p < 0.01$). The peat moisture is lower in SP and in MJ (slope = -1.322, $p < 0.01$).

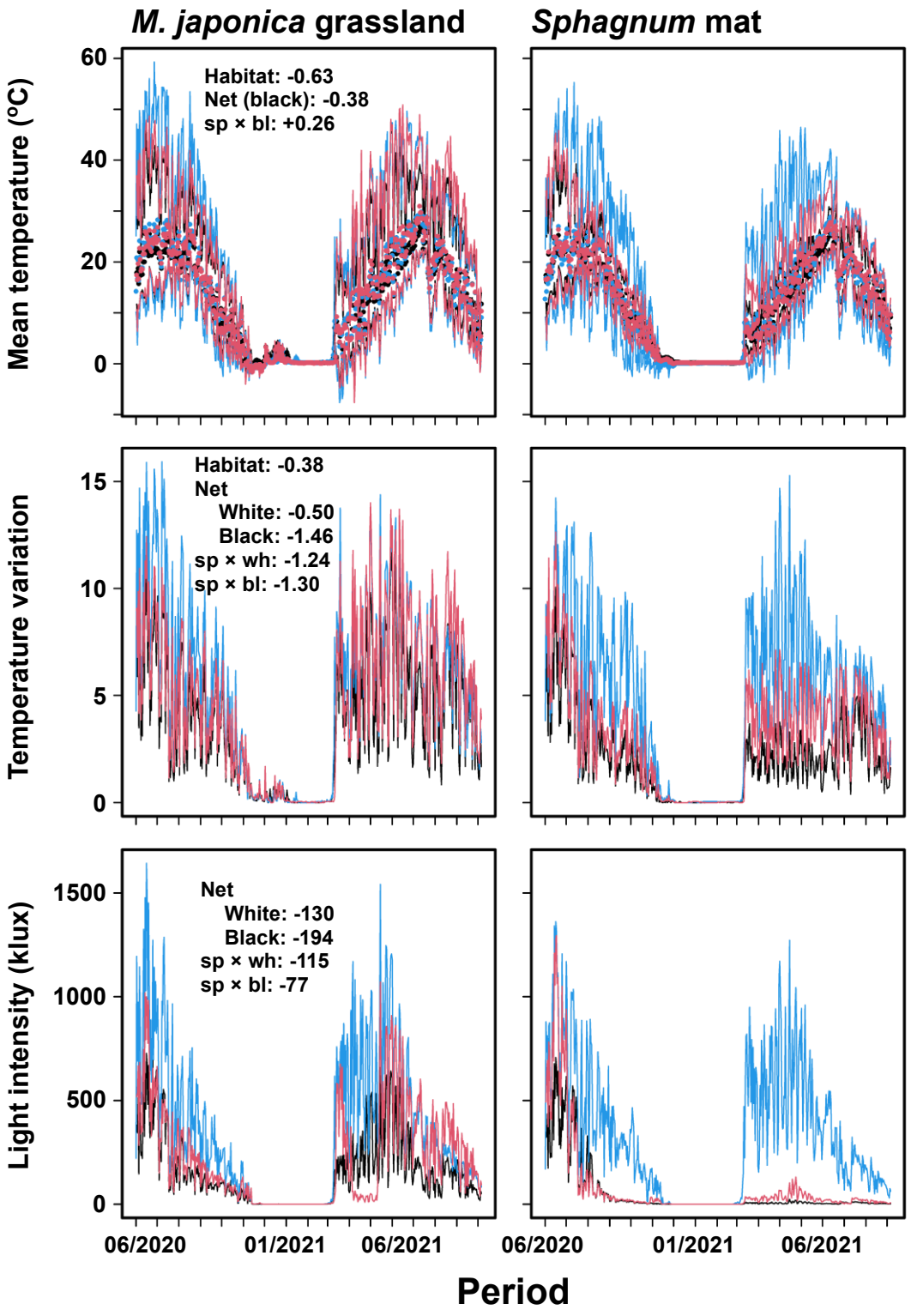

Fig 5 Daily mean temperature (°C), daily temperature fluctuation (SD) and daily cumulative light intensity (klux) under the manipulation of sunlight on *Moliniopsis japonica* grassland and *Sphagnum* mat in 2020 and 2021. The sunlight was intercepted by none (blue lines), white net (red lines) and black net (black lines). The dates on the x-axis are slightly changed to decrease the overlaps of symbols and lines. On the mean temperature, circles show the average. The upper and lower lines show the maximum and minimum temperatures, respectively. Mean temperature, temperature fluctuation and cumulative light intensity are compared between habitats and between nets with their interactions by GLMM.