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Precipitation regime controls bryosphere carbon cycling similarly across contrasting ecosystems

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In arctic and boreal ecosystems, ground bryophytes play an important role in regulating carbon (C) exchange between vast belowground C stores and the atmosphere. Climate is changing particularly fast in these high-latitude regions, but it is unclear how altered precipitation regimes will affect C dynamics in the bryosphere (i.e. the ground moss layer including senesced moss, litter and associated biota) and the closely associated upper humus layer, and how these effects will vary across contrasting environmental conditions. Here, we set up a greenhouse experiment in which mesocosms were assembled containing samples of the bryosphere, dominated by the feather moss *Hylocomium splendens*, and the upper humus layer, that were collected from across a boreal forest chronosequence in northern Sweden which varies strongly in nutrient availability, productivity and soil biota. We tested the effect of variation in precipitation volume and frequency on CO_2 exchange and dissolved organic carbon (DOC) export, and on moss growth. As expected, reduced precipitation volume and frequency lowered net CO_2 efflux, DOC export and moss growth. However, by regulating moisture, the lower bryosphere and humus layers often mediated how precipitation volume and frequency interacted to drive C dynamics. For example, less frequent precipitation reduced moss growth only when precipitation volume was low. When volume was high, high moisture content of the humus layer helped avoid moss desiccation. Variation in precipitation regime affected C cycling consistently in samples collected across the chronosequence, despite large environmental variation along the sequence. This suggests that the bryosphere exerts a strong buffering effect on environmental variation at the forest floor, which leads to similar responses of C cycling to external perturbations across highly contrasting ecosystems. As such, our study indicates that projected increases in droughts and ground evapotranspiration in high-latitude regions resulting from climate change will consistently reduce C losses from moss-dominated ecosystems.

Keywords: boreal forest, context-dependency, dissolved organic carbon, forest succession, moss, net ecosystem exchange

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Introduction

Climate is changing fastest in high-latitude (boreal and arctic) regions, where global models forecast an increase in the temporal heterogeneity of precipitation and in the occurrence of extreme precipitation events, as well as increased periods of prolonged droughts (Collins et al. 2013). Further, rapid warming will increase evapotranspiration rates and thus contribute to declines in moisture content at and below the ground surface (Collins et al. 2013, Berg et al. 2017). These changes in moisture content can affect nutrient and carbon (C) cycling (Wu et al. 2011, Öquist et al. 2014, Sierra et al. 2015), and thus impact the substantial amounts of C stored in high-latitude ecosystems, much of which is located at or near the ground surface (Jobbágy and Jackson 2000, Pan et al. 2011). Moreover, these high-latitude C stores are particularly sensitive to climate change (Gauthier et al. 2015, Koven et al. 2017). Given that the C balance in terrestrial ecosystems is largely driven by plant–soil microbe interactions (Metcalfe et al. 2011), the response of plant and microbial function to altered ground moisture regimes is likely to determine the extent to which high-latitude ecosystems will serve as a source or sink of C (Reichstein et al. 2013).

In most high-latitude ecosystems the ground vegetation is characterised by high abundances of bryophytes, often forming dense, continuous layers of mosses (Nilsson and Wardle 2005, Turetsky et al. 2012). Bryophyte communities on the soil surface form the basis of the bryosphere (sensu Lindo and Gonzalez 2010), a ground layer encompassing living and senescent (i.e. non-photosynthetic) moss, litter and the associated food web. The bryosphere can account for a substantial proportion of total ecosystem C uptake, especially in boreal and arctic ecosystems (Lindo et al. 2013, Street et al. 2013). For example, the bryosphere can account for more than 20% of net primary productivity (NPP) of the ground layer vegetation in boreal forests (Turetsky et al. 2012, Wardle et al. 2012). The bryosphere also contributes to soil C inputs by producing recalcitrant litter, which can represent a large proportion of the upper humus layer (Lang et al. 2009, Hilli et al. 2010, Jonsson et al. 2015), and controls decomposition by regulating ground temperature and moisture (Jackson et al. 2013, Sun et al. 2017) and nitrogen inputs (Lindo et al. 2013), making it an important driver of C cycling in high-latitude ecosystems.

Carbon cycling in moss-dominated ecosystems can be greatly impacted by predicted future changes in precipitation regime and ground evapotranspiration, as moisture is a major driver of physiological processes in mosses (Busby and Whitfield 1978, Metcalfe and Ahlstrand 2019). Moss moisture content is often highly dependent on frequent precipitation, especially in environments that lack high water levels (Kulmala et al. 2011, Nijp et al. 2014, Stuiver et al. 2014). As such, precipitation regimes leading to decreased ground layer moisture content are expected to impair gross primary productivity (GPP) of mosses, thus reducing C inputs to the ecosystem from recalcitrant moss litter. However, the high water holding capacity of the bryosphere and underlying soil can regulate how changes in precipitation affect moss moisture (Robroek et al. 2009, Nijp et al. 2014), and the bryosphere can reduce evaporation from soil (Beringer et al. 2001). Further, changes in moisture can also alter microbial activity in the bryosphere (Jackson et al. 2011, Gundale et al. 2012). Lower precipitation amounts are expected to impair both moss and heterotrophic respiration (i.e. ecosystem respiration, ER), and to reduce the loss of dissolved organic carbon (DOC) in leachates (Öquist et al. 2014). Meanwhile, changes in precipitation frequency that lead to increased drying–rewetting cycles can promote the release of DOC in leachates from mosses (Slate et al. 2019) and from soil (Gordon et al. 2008). Therefore, projected shifts in precipitation regime due to climate change could potentially alter both C uptake and C loss in moss-dominated ecosystems, with potential consequences for ecosystem C cycling and C storage. However, the effect of precipitation regime on C dynamics in moss-dominated ecosystems, and how this depends on environmental context, has been little explored.

In boreal forests, which account for 30% of the global forest area and are one of the largest stores of terrestrial C (Pan et al. 2011, Bradshaw and Warkentin 2015), bryosphere function can vary greatly across contrasting environmental conditions. For example, moss NPP and the decomposer community of the forest floor, including in the bryosphere, can vary in response to the dominant trait spectra of the plant community, light availability, nutrient availability and forest successional stage. Notably, the food web of the bryosphere and the closely associated upper humus layer is more fungal-based in late- compared to early-succession boreal forests (Clemmensen et al. 2015, Jonsson et al. 2015). Because fungal-based food webs are better able to adapt to changes in moisture availability than are bacterial-based food webs (de Vries et al. 2012), the effect of changes in precipitation regime on decomposition in moss-covered forest floors may depend on successional stage. Further, moss NPP increases as forest succession proceeds (Jonsson et al. 2015), in part supported by higher rates of nitrogen fixation by moss-associated cyanobacteria (Lagerström et al. 2007, Gundale et al. 2012, Bay et al. 2013). Nitrogen fixation rates are sensitive to variation in precipitation regime (Jackson et al. 2011), particularly in late-successional forests, where less precipitation leads to greater declines in nitrogen fixation rates than in early-successional forests (Gundale et al. 2009). Therefore, successional stage may mediate the effects of precipitation regime on bryosphere C uptake.

Here, we used a greenhouse mesocosm experiment to examine the effects of variation in water addition (intended to mimic different precipitation regimes) on bryosphere and upper humus C cycling across contrasting forested ecosystems. For this, we created mesocosms from moss-covered forest floor samples (consisting of *Hylocomium splendens* mats and the top humus layer) collected from 30 lake islands that collectively comprise a well-characterised post-fire chronosequence in the boreal-forested zone of northern Sweden. These islands vary greatly in area and thus fire history; larger islands are intercepted more often by lightning than are smaller ones meaning that time since fire increases as islands become smaller (Wardle et al. 1997, 2003, 2012). With decreasing island size (and increasing time since fire), soil nutrient availability declines, leading to changes in the plant community towards species with more resource-conservative functional traits and impairment of decomposition processes (Wardle et al. 2003, 2012, Clemmensen et al. 2015). Further, their decomposer communities are more resource-acquisitive (i.e. more bacterial-based) on early-successional (larger) islands, and more resource-conservative (i.e. more fungal-based) on late-successional (small) islands (Wardle et al. 2012, Clemmensen et al. 2015).

To assess how frequency and volume of precipitation interact to drive C cycling in moss-dominated ecosystems, and whether these effects depend on their nutrient and microbial status, we tested the following hypotheses: 1) lower volume and frequency of water addition will decrease moss growth, gross primary productivity (GPP) and ecosystem (i.e. bryosphere and humus) respiration (ER), because drier conditions will impair moss photosynthesis, and moss and microbial respiration. Since non-photosynthetic biomass often dominates moss-covered ecosystems (Lindo and Gonzalez 2010), ER will decrease more than GPP, leading to lower net CO_2 loss (i.e. lower net ecosystem exchange, NEE). Reduced water addition frequency will have a greater effect at lower water addition volumes, because it will lead to more severe desiccation. 2) Lower volumes of water addition will result in less leaching, while more intense drying–rewetting cycles from reduced frequency of water addition will increase the concentration of dissolved organic carbon (DOC) in the leachates and thus increase DOC export. 3) Reduced volume and frequency of water addition will cause a greater reduction in moss GPP and moss growth in small compared to large islands. This is because the mosses in small islands are less limited by nitrogen availability due to greater rates of nitrogen fixation that are characteristic of later-successional ecosystems (Lagerström et al. 2007, Bansal et al. 2012). Conversely, the decrease in ER and DOC export in response to lower volume and frequency of water addition will be greater in large compared to small islands. This is because microbial communities in the humus layer, which likely dominate moss-covered forest floor respiration, are more resource-acquisitive (e.g. bacterial-based) on large islands and therefore more sensitive to variation in moisture content (Clemmensen et al. 2015). By testing the response of total C loss (i.e. from net CO_2 loss and DOC export) to reduced water addition volume and/or frequency, we aimed to better understand the effect of changes in precipitation regime on the C balance of moss-dominated ecosystems, and how this effect may depend on environmental context.

Methods

Sampling site

We collected samples of the bryosphere and upper humus from 30 forested lake islands in northern Sweden (lakes Hornavan and Uddjaure, 65°57′–66°10′N, 17°43′–17°52′E). Mean air temperature is +13°C in July and −14°C in January, and mean annual rainfall is 750 mm. All islands formed about 9000 years ago following the retreat of land ice, and the only major extrinsic factor that varies between the islands is wildfire frequency. Larger islands intercept more lightning strikes and are thus subjected to more frequent stand-replacing fires than are the smaller islands; time since the most recent fire across the 30 islands ranges from 60 to 5000 years (Wardle et al. 2003). As island size decreases and time since fire increases, there is a decline in soil fertility that leads to successional changes in plant and microbial communities (Clemmensen et al. 2015, Kumordzi et al. 2015). As such, the more resource-conservative plant communities on smaller islands are less productive and produce more recalcitrant litter than do those on large islands (Lagerström et al. 2013), and the more resource-conservative microbial communities on small islands produce more recalcitrant necromass (Clemmensen et al. 2013), leading to slower organic matter decomposition (Wardle et al. 2003). Consistent with previous work in this study system (Wardle et al. 2003, 2012, Fanin et al. 2018, Kardol et al. 2018, Grau-Andrés et al. 2020) we grouped the 30 islands into three size classes with ten islands in each class: large (> 1.0 ha, mean time since fire ± SE: 585 ± 233 years), medium (0.1–1.0 ha, mean time since fire: 2180 ± 385 years) and small (< 0.1 ha, mean time since fire: 3250 ± 439 years). Further details of environmental variation across the island size gradient is given in Supporting information.

Sample collection and experimental design

Four samples of the moss-covered forest floor were collected from each of the 30 islands ($n = 120$) between 30 July and 16 August 2018 using a 10.3-cm internal diameter corer fitted with a serrate edge. Sampling locations were randomly chosen among continuous moss layers dominated by *Hylocomium splendens*, which is the most abundant moss species across all three island size classes and forms large monospecific patches (Lagerström et al. 2007). We focused on moss layers dominated by a single moss species to minimise heterogeneity of the bryosphere structure in the mesocosms, and thus minimise sources of variation other than our experimental treatments. The samples included the living and senesced part of the moss (mean height ± SD was 4.3 ± 1.1 cm) and the upper 5.7 ± 1.1 cm of the humus layer (Oi and/or Oe organic soil horizons, where organic matter is slightly or moderately decomposed; Soil Survey Staff 2015). While moss and humus thickness of the samples measured in the field did not vary between island size classes, humus biomass measured at the final harvest varied across island size classes and was slightly higher for small islands (3.4 ± 0.2 kg m^{-2}) than for medium (2.7 ± 0.2 kg m^{-2}) and large islands (2.4 ± 0.1 kg m^{-2}; $F_{2,27} = 5.0$, $p = 0.01$; Supporting information). The transition from partly decomposed moss to partly decomposed humus was gradual, with no sharp boundary between the moss and the humus layer. Assessing ecosystem functions in moss-dominated forest floors requires that the bryosphere and the underlying humus are jointly examined, as moss litter is a major constituent of upper humus layers (Hilli et al. 2010), and both are intimately linked in controlling C dynamics (Lindo and Gonzalez 2010). The upper humus layer contributes to high CO_2 and water vapour partial pressures in the moss layer (Carleton and Dunham 2003, DeLucia et al. 2003), and mosses supply carbon and nutrients to the soil biota (Sun et al. 2017, Slate et al. 2019).

Upon collection, the samples were put in PVC cylinders (10.3 cm internal diameter, 10 cm height) fitted with a permeable bottom made out of gardening cloth. These mesocosms were covered with translucent, permeable gardening cloth and kept moist at ambient temperature for 2–19 days, and then stored at 4°C for 18 days. On 6 September 2018, the mesocosms were transported to a greenhouse and subjected to one of four water addition treatments until 20 December 2018 (104 days). Day length at the greenhouse was set to 18 h, and photosynthetic active radiation (PAR) during the day-time was 170 ± 18 μmol m^{-2} s^{-1} at the top of the mesocosms. Mean day-time temperature was 21.9 ± 0.9°C, while night-time temperature was 16.3 ± 0.8°C. Mean day-time relative humidity was 67.9 ± 5.6%, while night-time relative humidity was 74.5 ± 3.6%.

Water addition treatments

Each of the four mesocosms per island was assigned to one of four water addition treatments. The treatments were a factorial combination of two levels of water addition volume (average volume per mesocosm per day across the experimental period, either 20 ml or 5 ml) and two levels of water addition frequency (either every two days or every four days). The higher watering volume (20 ml day^{-1} per mesocosm, which corresponded to 2.4 l m^{-2} day^{-1}) and frequency (every two days) represented the approximate mean summer (June–September) precipitation regime (volume 2.2 l m^{-2} day^{-1}, frequency 1.7 days) at the sampling site between 1980 and 2010 (SMHI 2020), i.e. 'ambient' conditions. The lower volume (0.6 l m^{-2} day^{-1}) and frequency (every four days) treatments aimed to represent lower ground moisture due to projected longer droughts and increased ground evaporation in the region resulting from climate change (Jackson et al. 2011, Stuiver et al. 2014). We used rain water collected in the vicinity of the greenhouse (DOC = 1.8 ± 0.1 mg C l^{-1}, dissolved nitrogen = 0.15 ± 0.03 mg N l^{-1}, n = 3), and applied it to the mesocosms using a spray bottle. The mesocosms were loosely covered with a gardening mesh (allowing 88% light transmittance) to lower evaporation rates and thus simulate the insulating effect of understory dwarf shrub and tree canopy cover on evaporation from the bryosphere (Heijmans et al. 2004).

We monitored variation in moss moisture content across each watering cycle in all mesocosms from day 87 to day 91 after starting the experiment. To do this in a manner that minimised disturbance to the mesocosms, we visually estimated the proportion of 'wet' versus 'dry' moss tissue in each mesocosm daily from 1 h after each water addition to just before the next water addition (i.e. 0, 1 and 2 days after water addition in ambient frequency treatments, and 0, 1, 2, 3 and 4 days after water addition in low frequency treatments). Representative 'wet' and 'dry' moss shoots (top 2 cm) from 15 randomly-chosen mesocosms (3–5 from each water addition treatment) were then sampled to calculate moisture content gravimetrically. We then used the measurements from these representative shoots to estimate moss moisture content for all shoots in all mesocosms. Mesocosm-averaged moss drying rates were calculated by subtracting the estimated moss moisture content two days after water addition from the moisture content just after water addition. To further assess the effect of the water addition treatments on humus moisture content, we collected at the same time small samples (0.1 ± 0.04 g dry weight) of the top and bottom 2 cm of the humus layer, both just before and 1 h after water addition, once from each mesocosm (n = 480) to calculate moisture content gravimetrically.

CO_2 fluxes

We measured bryosphere CO_2 flux using a clear plastic chamber (light transmittance = 92%, dimensions = 12.35 × 12.35 × 16.05 cm) equipped with a CO_2 analyser, on each mesocosm and on each of four sampling dates (i.e. 44, 64, 84 and 104 days after the start of the experiment). To do this, we sealed the chamber to the top of each mesocosm and recorded headspace CO_2 concentrations every 15 s for about 4 min. A 5 cm diameter fan (4800 rpm, air flow = 0.25 m^3 min^{-1}) mixed the air in the chamber during measurements. The flux of CO_2 was calculated as the initial rate of change in CO_2 concentration over time by fitting either a non-linear or a linear model following Pedersen et al. (2010), as implemented in the package 'HMR' (Pedersen 2020) in R software (ver. 3.6.2; <www.r-project.org>). We discarded the first 15–30 s of each measurement to avoid unrepresentative values arising from sudden pressure differences when sealing the chamber to the mesocosms. For each of the four sampling dates and for each mesocosm we first estimated net ecosystem exchange (NEE; measured with the chamber uncovered) and then immediately thereafter, ecosystem respiration (ER; measured with the chamber covered with an opaque plastic sheet). The chamber was ventilated for at least 40 s between the NEE and ER measurements. Gross primary productivity (GPP) was calculated as NEE minus ER. Positive flux values indicate a net flux of CO_2 to the atmosphere, and negative values indicate net CO_2 uptake by the mesocosms (Chapin et al. 2006). We performed these measurements twice at each sampling date. First we performed them shortly before carrying out the water addition treatment, i.e. at the driest extreme of the treatment. We then repeated them about 1 h after carrying out the water addition treatment (to minimise transient responses of photosynthesis and respiration; Proctor et al. 2007), i.e. at the wettest extreme of the treatment. For each mesocosm at each sampling date, we averaged the CO_2 fluxes measured before and after watering to obtain a flux representative of the entire watering cycle.

Dissolved organic carbon

To estimate C loss from leached dissolved organic carbon (DOC), we recorded leachate volumes 30 min after each water addition event for each mesocosm in collection trays underneath the mesocosms. In addition, at each of the four sampling dates (44, 64, 84 and 104 days after the start of the experiment), we measured DOC concentration in leachates from each of the mesocosms that had produced leachates. To do this, about 10 ml of leachate were filtered through a 0.45 μm syringe filter at the time of collection and stored at 4°C for 5–14 days before analysis of total organic C using a Shimadzu TOC-V + TNM-1. Sample mishandling caused three missing observations out of a total of 240. For each sampling date and mesocosm, we calculated DOC export by multiplying the accumulated mesocosm leachate export over the previous 20 days (i.e. the length of time between sampling dates) by the corresponding leachate DOC concentration.

Total carbon loss

The two most important components of the net C balance of boreal forests are CO_2 fluxes and export of dissolved C (which is about 11% of the net CO_2 exchange; Öquist et al. 2014). We therefore combined data for CO_2 fluxes and C loss from DOC to calculate total C loss from each mesocosm during the experiment following Eq. 1. Daily CO_2 loss was calculated as the sum of NEE (i.e. net CO_2 flux in light conditions, which lasted for 18 h in our experiment) and ER (i.e. net CO_2 flux in dark conditions, which lasted for 6 h).

$$\begin{aligned}\text{Total C loss}\left(\text{mg C m}^{-2}\ \text{d}^{-1}\right) = {} & \left(\text{NEE}\left(\text{mg C m}^{-2}\ \text{h}^{-1}\right)\times 18\ \text{h}\right) \\ & + \left(\text{ER}\left(\text{mg C m}^{-2}\ \text{h}^{-1}\right)\times 6\ \text{h}\right) \\ & + \left(\text{leachate export}\left(\text{lm}^{-2}\ \text{d}^{-1}\right)\times[\text{DOC}]\left(\text{mg Cl}^{-1}\right)\right)\end{aligned} \quad (1)$$

Moss growth

To estimate moss growth over the duration of the experiment, we marked a reference point at the stem of five moss shoots per mesocosm at the beginning of the experiment using a waterproof writing correction fluid (Tipp-Ex). As *H. splendens* grows in annual segments on the previous year shoot (Okland 1995), we marked each stem below the topmost segment to standardise the measurements. We then measured the distance from the reference point to the apex of the shoot (i.e. the terminal growing bud) using calipers. This distance was re-measured towards the end of the experiment (i.e. after 79–83 days) and subtracted from the initial measure to locate the new growth. This new growth was then clipped, oven-dried and weighed to derive a mesocosm-averaged measure of moss growth.

Final harvest

At the end of the experiment (20–21 December 2018) we harvested the moss layer (including photosynthetic and non-photosynthetic moss) and the humus layer and calculated their oven-dry weight.

Statistical analyses

We analysed all data using linear mixed effects models (package *nlme*; Pinheiro et al. 2018) in R. We analysed GPP, ER and NEE (separately for measurements before watering, after watering, the mean of the two and their difference (i.e. fluxes after watering minus before watering)), and total C loss, by specifying as fixed effects the main and interactive effects of water addition volume, frequency, island size class and time since the start of the experiment. Since biological responses to time are often nonlinear, time was entered in the models as a categorical variable, i.e. we modelled the mean response in each of four time points, for each combination of water addition treatment and island size class (Liu et al. 2012, Barton and Ives 2014). Mesocosm nested within island identity was included as a random effect to account for spatial non-independence among the four mesocosms from each island. Additionally, we defined a correlation structure (function 'corCAR1') using time since start (as a continuous variable) to account for the repeated measurements. For ER, NEE and total C loss, total biomass was also included as a covariate to account for differences in biomass between mesocosms. Statistical analyses of leachates were limited to the high-volume water addition treatments because low-volume water addition treatments did not produce any leachates. For analysis of leachate export, DOC concentration and DOC export, we included as fixed effects the main and interactive effects of water addition frequency, island size class and time since the start of the experiment. As above, biomass was added as a fixed effect, mesocosm nested within island identity was included as a random effect, and time as a correlation structure.

We analysed daily moss moisture content by fitting as fixed effects the main and interactive effects of water addition volume, island size class and time since water addition. Separate models were fitted for ambient and for low water addition frequency treatments because the number of levels of the factor variable 'time since water addition' differed, in that measurements were made immediately after and 1 and 2 days after watering (ambient frequency), and immediately after and 1, 2, 3 and 4 days after watering (low frequency). Mesocosm nested within island identity was included as a random effect, and time since water addition as a correlation structure to account for the repeated measurements. We analysed humus moisture content measured immediately before and immediately after water addition by fitting as fixed effects the main and interactive effects of water addition volume, frequency, island size class and time since water addition (i.e. either immediately before or immediately after water addition). Separate models were fitted for the top and for the bottom humus layer to facilitate interpretation, as our focus was on moisture differences within bryosphere layers. Mesocosm nested in island identity was included as a random effect, and time since water addition as a correlation structure. Finally, variables that were measured only once per mesocosm (i.e.

moss drying rates, moss growth, initial moss layer thickness and humus biomass) were analysed by fitting the main and interactive effects of water addition volume, frequency and island size as fixed effects, and island identity as a random effect.

We checked model assumptions by plotting residuals against fitted values, and used a constant variance function ('varIdent') to account for variance heterogeneity among precipitation treatments when appropriate (Zuur et al. 2009). Analysis of DOC concentration and DOC export also required a log transformation of the response variable to homogenise the variance. Pairwise comparisons between factor levels were computed using the package *emmeans* (Lenth 2020). The variance explained by the fixed effects (i.e. marginal R^2) and the variance explained by both fixed and random effects (i.e. conditional R^2) were computed using the function 'r.squaredGLMM' in the package *MuMIn* (Barton 2019).

Results

Moisture dynamics

Moss moisture content during each watering cycle decreased much faster with time when the volume of water addition was low, compared to the water addition treatment that represented ambient levels (Fig. 1a–d; Supporting information). Island size mediated the effect of water addition volume on moss drying rates (interaction $F_{2,81} = 4.6$, $p = 0.01$; Supporting information): under ambient volumes of water addition, moss dried out fastest in samples from large islands (moss lost 17.3 ± 35.2% of moisture (dry weight basis; median ± interquartile range) day^{-1}), and slowest in samples from small islands (2.7 ± 8.0% day^{-1}), but island size had no effect on moss dying rates under low volumes of water addition. Moisture content of the humus layer was substantially higher for the ambient compared to low volume water addition treatments, and generally either decreased slightly or remained constant during the watering cycle (Fig. 1e–l; Supporting information). The effect of water addition frequency on humus moisture content was mediated by water addition volume: less frequent watering increased humus moisture content at low volumes, but had no effect at ambient volumes. Island size had no main or interactive effect on the moisture dynamics of the upper or lower humus layer.

CO_2 fluxes and moss growth

Water addition regime affected gross primary productivity (GPP) of moss consistently across the island size gradient

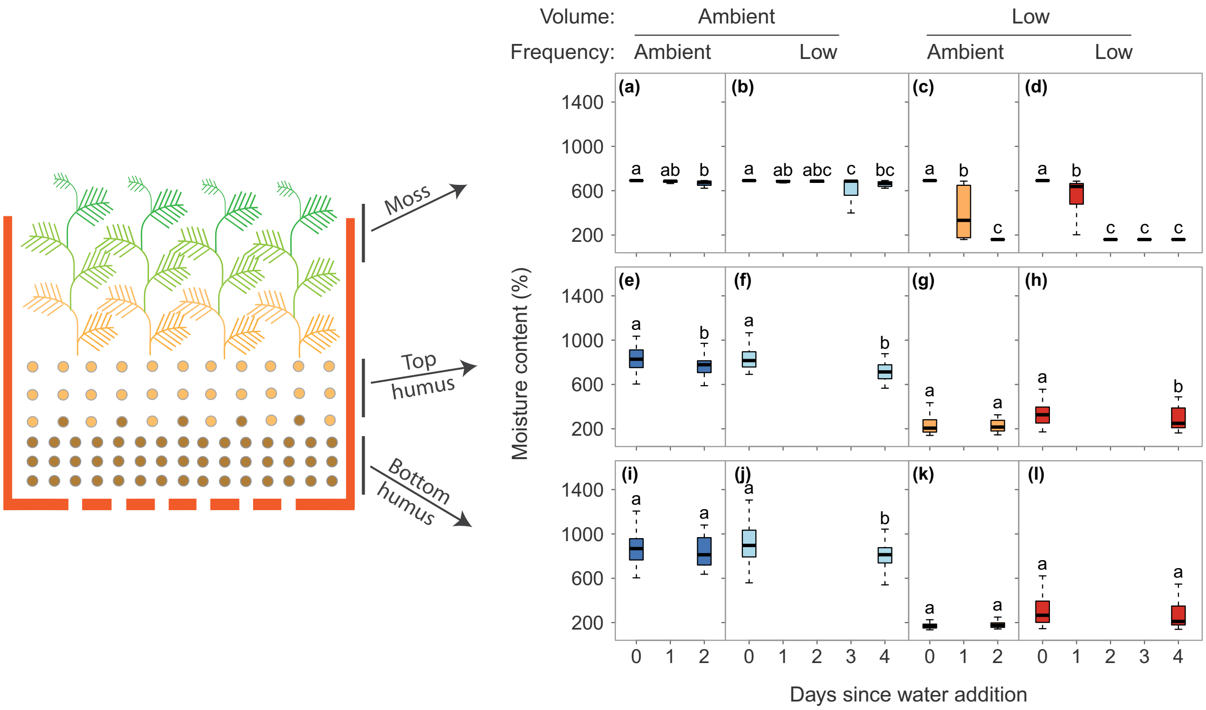

Figure 1. (Left) Diagram of the bryosphere structure in the mesocosms. (Right) Moisture content (in % dry weight basis) of the upper 2 cm of the moss layer (panels a–d), upper 2 cm of the humus layer (panels e–h) and bottom 2 cm of the humus layer (panels i–l) during each water addition treatment, i.e. from just after to just before two consecutive water addition events. Boxes and whiskers represent the interquartile range and the outermost values within 1.5 times the interquartile range, respectively; thick lines within boxes represent the median. In each boxplot, n = 30 (3 island size classes × 10 replicates). Within panels, same letters indicate that differences are not statistically significant (post hoc comparisons based on Tukey's test, α = 0.05). Results of models underpinning the statistical testing are provided in Supporting information.

(Supporting information). Averaged across all island sizes, moss GPP decreased with both lower water addition volume (by mean ± SD = 17 ± 35 mg C m^{-2} h^{-1}) and lower water addition frequency (by 8 ± 37 mg C m^{-2} h^{-1}), but there was no interaction between these two factors (Fig. 2c, Supporting information). The decrease in GPP in response to low water addition volume was more apparent before water addition (i.e. when moss was driest) than after water addition (Fig. 2a–b). Similar to GPP, moss growth was impaired by reduced volume and frequency of water addition consistently across the island size gradient (Fig. 3, Supporting information). On average, lower frequency had a greater effect on reducing moss growth at ambient compared to low volumes of water addition.

Ecosystem respiration (ER) of the bryosphere and humus also responded to water addition regime consistently across the island size gradient. Across all island sizes, ER was on average 53 ± 35 mg C m^{-2} h^{-1} higher in mesocosms subjected to ambient compared to low volumes of water addition (Fig. 2c, Supporting information). The effect of frequency of water addition on ER was mediated by the volume of water addition, because lower frequency slightly decreased ER at ambient volumes but strongly increased ER at low volumes. This pattern was more apparent after water addition than before water addition (Fig. 2d–e). Similar to ER, lower water addition volume decreased net ecosystem exchange (NEE) (i.e. reduced CO_2 efflux), and volume mediated the effect of frequency: lower frequency had no effect on NEE at ambient volume, but increased NEE at low volume (Fig. 2i, Supporting information). Island size did not mediate the response of NEE to variation in water addition volume or frequency.

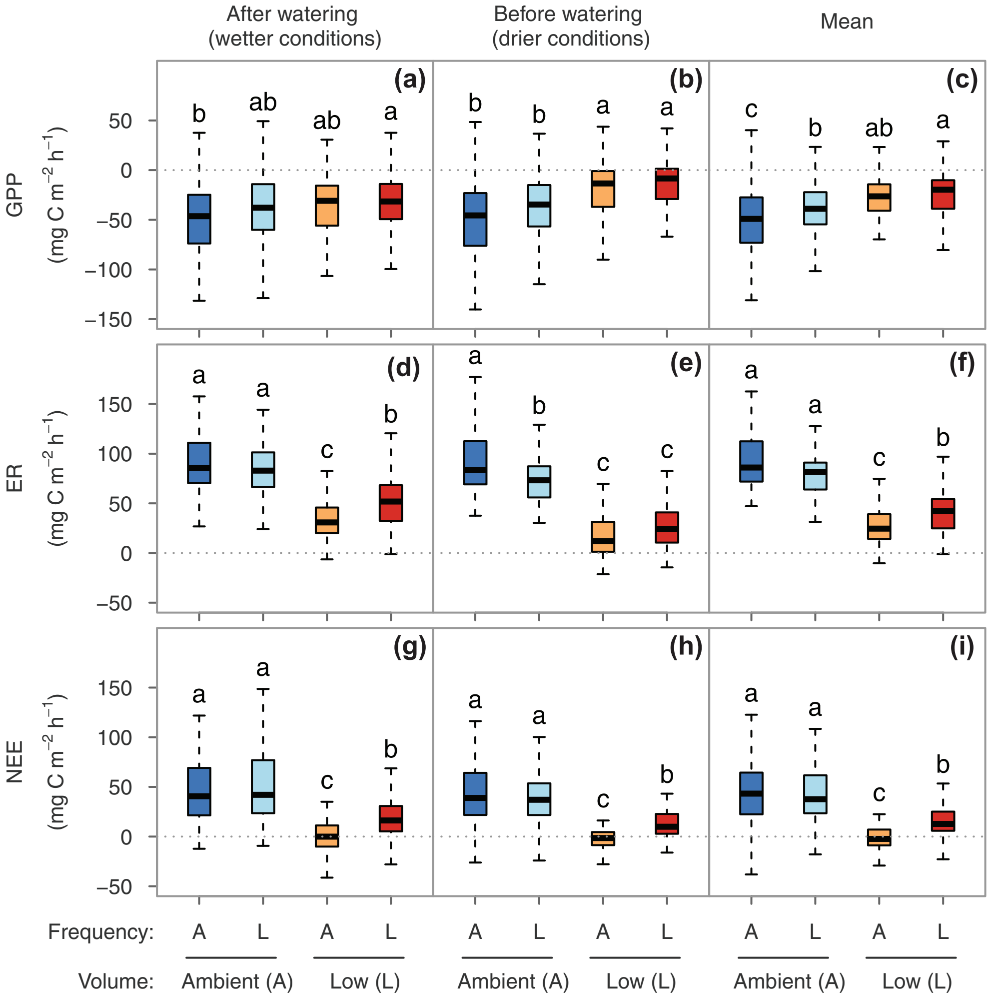

Figure 2. Mesocosm CO_2 fluxes (ecosystem respiration, ER; gross primary productivity, GPP; and net ecosystem exchange, NEE) across each combination of water addition volume and frequency, for measurements taken before and after water addition, and their mean. Positive values indicate a net flux of CO_2 to the atmosphere, and negative values, a net CO_2 uptake by the mesocosms. Boxes and whiskers represent the interquartile range and the outermost values within 1.5 times the interquartile range, respectively; thick lines within boxes represent the median. Data were aggregated across all island size classes because there was no effect of island size class. In each boxplot, n = 120 (3 island size classes × 10 replicates × 4 time points). Within panels, same letters indicate that differences are not statistically significant (post hoc comparisons based on Tukey's test, $\alpha = 0.05$). Model details are provided in Supporting information.

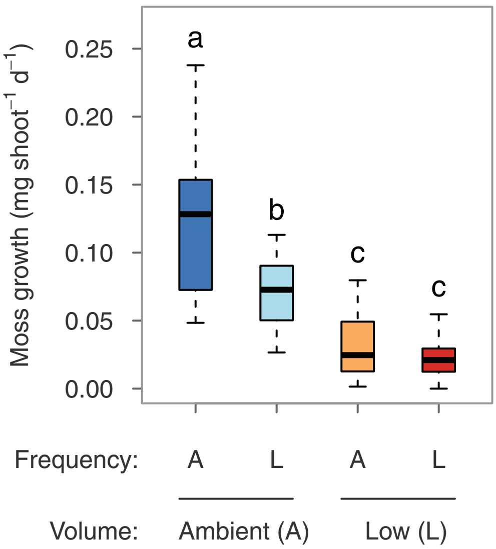

Figure 3. Moss shoot biomass production over the duration of the experiment, for each combination of volume and frequency of water addition. Boxes and whiskers represent the interquartile range and the outermost values within 1.5 times the interquartile range, respectively; thick lines within boxes represent the median. Data were aggregated across all island size classes because there was no effect of island size class. In each boxplot, n = 30 (3 island size classes × 10 replicates). Same letters indicate that differences are not statistically significant (post hoc comparisons based on Tukey's test, $\alpha = 0.05$). Model details are provided in Supporting information.

The immediate response of moss GPP to water addition (i.e. increase in CO_2 uptake relative to pre-water addition) varied over the duration of the experiment, and this relationship was mediated by the frequency of water addition. Under ambient water addition, the response of moss GPP to rewetting increased with time, while under low water addition the response of moss GPP decreased with time (Supporting information). The immediate response of ER was also affected by an interaction between time and water addition frequency. Under ambient water addition frequency, the response of ER to rewetting did not change with time. Yet, when frequency was reduced, ER response to rewetting decreased with time (Supporting information). Further, island size class mediated the effect of frequency on the immediate response of GPP and ER to water addition. Under ambient water addition frequency, island size had no effect, but when frequency of water addition was low, rewetting induced the weakest GPP and ER recovery in small islands (Supporting information).

Dissolved organic carbon

Leachates were only exported from mesocosms that received ambient water addition volumes (Fig. 4a). For these treatments, the effect of variation in water addition frequency on leachate export, DOC concentration or DOC export did not differ between island size classes (Supporting information). Overall, lower frequency of water addition had no effect on leachate export, DOC concentration or DOC export (Fig. 4). While island size had no main effect on leachate export or DOC concentration, DOC export was larger ($F_{2,27} = 3.6$, $p = 0.04$) in samples from medium islands (207 ± 184 mg C m^{-2} day^{-1}) than in samples from small islands (118 ± 55 mg C m^{-2} day^{-1}), and was intermediate for samples from large islands (155 ± 147 mg C m^{-2} day^{-1}).

Total carbon loss

Total bryosphere C loss was largely driven by CO_2 efflux, with DOC only contributing to 5 ± 6% of the C loss overall and 10 ± 4% at ambient volumes of water addition (Fig. 5). Similar to our findings for ER and NEE, island size had no

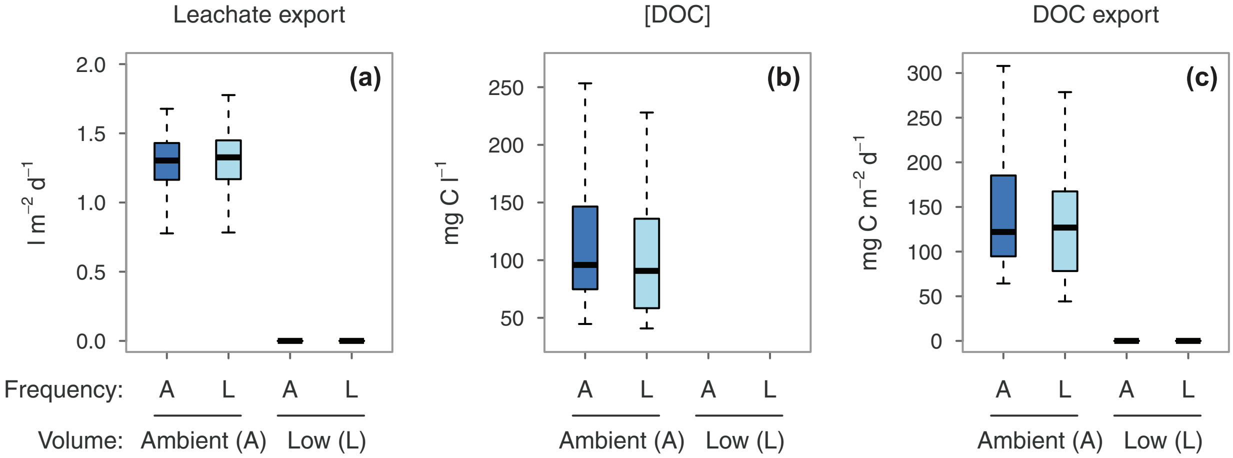

Figure 4. Leachate export, concentration of dissolved organic carbon (DOC) in the leachate, and DOC export across each combination of water addition volume and frequency. Boxes and whiskers represent the interquartile range and the outermost values within 1.5 times the interquartile range, respectively; thick lines within boxes represent the median. Data were aggregated across all island size classes because frequency did not interact with island size class. In each boxplot, n ranged from 118 to 120 (3 island size classes × 10 replicates × 4 time points). Frequency of water addition had no effect on any of the three variables (post hoc comparisons based on Tukey's test, $\alpha = 0.05$). Model details are provided in Supporting information.

overall effect on total C loss, and did not mediate the effect of water addition regime on total C loss. Also in line with the CO_2 flux results, total C loss decreased in response to lower volume of water addition, while lower frequency had no effect at ambient volumes but increased total C loss at low volumes (Fig. 5, Supporting information).

Discussion

Using a mesocosm experiment, we found that precipitation volume and frequency, and their interaction, controlled C dynamics in the bryosphere and upper humus layer, with those treatments that caused drier conditions generally resulting in a decrease in net CO_2 efflux and DOC export. These effects were largely consistent for mesocosms originating from highly contrasting ecosystems across a boreal forest successional gradient. Below, we examine our findings and discuss how they contribute to our understanding of forest floor C dynamics under changing precipitation regimes.

CO_2 fluxes and moss growth

In line with our first hypothesis, bryosphere gross primary productivity (GPP) and moss growth were impeded by lower volume and frequency of water addition. Volumes of water addition representing ambient precipitation regimes generally kept moss moisture content above 600%, i.e. close to the moisture content of *Hylocomium splendens* at field capacity, and above the 200–250% threshold below which *H. splendens* GPP rapidly declines (Busby and Whitfield 1978, Skre et al. 1983). Conversely, low volumes of water addition led to quick declines in moss moisture content (i.e. it averaged 479% one day after watering and 200% two days after) and thereby impaired moss GPP and growth. Although *H. splendens* has a limited capacity to regulate internal moisture content and is therefore sensitive to precipitation frequency (Kulmala et al. 2011, Gundale et al. 2012), the uppermost bryosphere layer remained wet for up to four days after ambient volume water addition. This suggests that the relatively wet lower layer of the bryosphere (i.e. the senesced moss) and underlying humus layer in ambient volume water addition treatments helped the upper photosynthetic part of the bryosphere avoid desiccation. Possible mechanisms of upward moisture transfer include evaporation from the wetter lower layers followed by condensation on the moss shoots, external capillary wicking and some (though limited) internal transport through cell cytoplasm or cell wall (Carleton and Dunham 2003, Price et al. 2009, Sokołowska et al. 2017). While moss growth was influenced by an interactive effect of water addition volume and frequency, the increase in moss growth with higher frequency was greatest at higher volumes of water addition, contrary to findings in peatlands (Robroek et al. 2009, Nijp et al. 2014). However, in line with our results, previous work on boreal feather mosses has found that rates of litter decomposition and cyanobacterial nitrogen fixation in the bryosphere responded most strongly to increased frequency of water addition at higher precipitation volumes (Jackson et al. 2011). Together, this suggests that variation in frequency of water addition when moisture is below a minimum threshold has a negligible effect on moss function, and that consideration of both precipitation volume and frequency is key to understanding how altered precipitation regimes affect bryosphere C uptake.

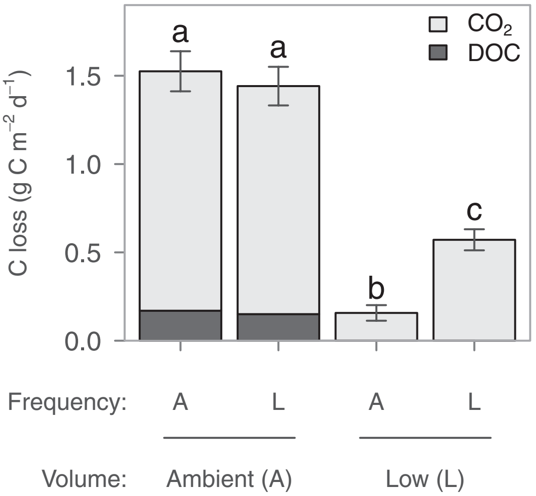

Figure 5. Total carbon loss (including CO_2 efflux and leachate dissolved organic carbon, DOC) for each combination of volume and frequency of water addition. Error bars are SE computed on mesocosm-averaged values ($n=30$ in each water addition treatment; 3 island size classes × 10 replicates). Data were averaged across all island size classes because there was no effect of island size class. Same letters indicate that differences are not statistically significant (post hoc comparisons based on Tukey's test, $\alpha=0.05$). Model details are provided in Supporting information.

Ecosystem respiration (ER) of the bryosphere and upper humus layer also decreased in response to lower water addition volume, presumably through impairment of both autotrophic and heterotrophic respiration (i.e. decreased rates of organic matter decomposition) (Wu et al. 2011, Sierra et al. 2015). Contrary to our first hypothesis that less frequent water addition would impair ER, lower frequency had no effect on ER at ambient water addition volumes and promoted ER at low water addition volumes. The lack of effects of watering frequency at ambient volumes can be explained by the small effect of frequency on overall bryosphere and humus moisture content, which remained high throughout the watering cycle. In contrast, less frequent water addition in low volume addition treatments led to wetter humus, possibly due to reduced water interception by mosses on top of the humus when a given amount of water was added less frequently but in larger amounts. As such, when precipitation volumes are low, evaporation in the upper moss layer is likely to prevent moisture from reaching the lower layers of the bryosphere and the humus especially when water addition is spread more evenly over time (Soudzilovskaia et al. 2011). Additionally, lower frequency of water addition (i.e. with fewer but larger watering events) could have led to greater leaching of soluble C and nitrogen from mosses into the humus which may have then stimulated microbial activity and increased ER in the humus (Sun et al. 2017, Slate et al. 2019). In total, these results indicate that respiration may have been mainly driven by moisture dynamics in the lower layers of the bryosphere and the upper humus.

Net ecosystem exchange (NEE) was dominated by ER and therefore showed similar patterns to ER. Lower volume of water addition decreased NEE (i.e. net CO_2 efflux from the bryosphere and upper humus layer was reduced), and less frequent water addition increased NEE only at low volumes of water addition. Ecosystem respiration dominated NEE responses to changes in water addition regime because total non-photosynthetic biomass contributing to ER was greater than photosynthetic moss biomass contributing to GPP, in alignment with our first hypothesis. Moreover, ER was more sensitive to changes in water addition regime than was GPP. For example, treatment-level mean ER ranged from 28 to 94 mg C m^{-2} h^{-1}, while GPP only ranged from 25 to 50 mg C m^{-2} h^{-1}. This could result from greater between-treatment differences in moisture content in the humus layer (where most respiration occurs) compared to the upper moss layer (where photosynthesis occurs). Additionally, the higher sensitivity of heterotrophic respiration to variation in moisture content (especially in warmer conditions; Sierra et al. 2015) relative to *H. splendens* GPP (Busby and Whitfield 1978) could help explain why ER responded more strongly to variation in water addition than did GPP. Because watering regimes leading to drier conditions (i.e. overall reduced water addition volume, and reduced frequency at low volumes) impaired ER more than GPP, a drier bryosphere and humus resulted in a lower NEE (i.e. decreased CO_2 loss). Taken together, these findings indicate that under future climatic scenarios leading to a drier forest floor during the growing season, impaired respiration from the bryosphere and upper humus layer could reduce CO_2 efflux and thus reduce C loss from boreal forests.

DOC and total C loss

To estimate the effect of variation in precipitation regime on the C budget of the bryosphere and upper humus layer, we also analysed the export of dissolved organic carbon (DOC) in leachates. Low volumes of water addition were insufficient to saturate the mesocosms and leachate export was therefore only observed in ambient volume water addition treatments. This aligns well with the strong positive correlation found between precipitation amount and DOC export in boreal forests (Öquist et al. 2014). In ambient volume treatments, reduced frequency of water addition leading to more intense drying-rewetting cycles had no effect on DOC concentration in the leachates, contrary to our second hypothesis. This finding contrasts with studies reporting that drying-rewetting cycles increase DOC production from mosses (Slate et al. 2019) and soil (Gordon et al. 2008) through greater damage to plant and microbial cells. A likely explanation of our results is that in the ambient volume addition treatments, relatively stable wet conditions in the lower layers of the bryosphere and in the humus buffer against large moisture fluctuations, including in the upper moss layer. This suggests that the response of DOC loss from the boreal forest floor to variation in precipitation regime will be mainly determined by the volume of precipitation, through controlling the amount of leachate that is exported. In contrast, precipitation frequency will have a minor impact on the C concentration of those leachates because of the buffering effect of the bryosphere and upper soil layer on soil moisture variation.

We estimate that DOC loss contributed only about 5% of total C loss overall (i.e. across all treatments), meaning CO_2 uptake and efflux were the main drivers of the C balance of the bryosphere and upper humus. As such, the effect of water addition on total C loss largely mirrored the response of ER and NEE, i.e. total C loss decreased with lower volume of water addition, and increased with lower frequency of water addition only at low volumes.

Context-dependency

Bryosphere GPP and moss growth responded similar to water addition treatments for bryosphere and upper humus layer samples taken from across highly contrasting ecosystems, i.e. islands supporting forest at different successional stages (i.e. time since wildfire) and with different ecosystem properties. This finding is contrary to our third hypothesis predicting that the functioning of mosses from late-succession forests which are less nitrogen-limited (because they support higher rates of biological nitrogen fixation; Lagerström et al. 2007) would be more affected by lower moisture availability than would mosses from early-succession forests (Gundale et al. 2009). However, our results are in line with previous work in the same study system showing that the productivity to biomass ratio of *H. splendens* was relatively invariant across the forest successional gradient (Bansal et al. 2012). Given that the mosses are likely to be less nutrient limited in late-successional than in early-successional forests (Lagerström et al. 2007, Bansal et al. 2012), the similar responses of the moss GPP and growth to moisture treatments across our successional gradient indicate that the relationship of moss productivity with moisture is likely to be independent of nutrient availability or of its nutrient status.

Further, our finding that ER and DOC export responded consistently to water addition treatments across the chronosequence is contrary to our hypothesis that these largely microbially-driven fluxes would be more impaired by low moisture in early- compared to late-succession forests. We expected this because from previous studies we know that, compared to late-succession forests, microbial communities in the upper humus of early-succession forests are less nutrient-limited and more bacterial-based, which would make them more susceptible to low moisture (Wardle et al. 2012, Clemmensen et al. 2015). Moreover, ER and total C loss were unaffected by forest successional stage, which is in contrast to reports from the same study system of higher respiration in the uppermost humus (Wardle et al. 2012) and the whole forest floor (i.e. including the humus layer, understory vegetation and tree roots; Wardle et al. 2016) in early-successional forests. This indicates that, compared to the broader forest floor respiration, respiration of the bryosphere and upper humus layer remains relatively invariant across strong gradients of plant and microbial productivity and soil fertility.

Taken together, our results show that the effects of variation in precipitation regime on function of moss-dominated ecosystems are consistent across vastly contrasting environmental conditions, and point to a buffering effect of the bryosphere on environmental variation among different ecosystems. This buffering effect could result from the high capacity of the bryosphere to retain nutrients (Liu et al. 2020), regulate microclimate (Jackson et al. 2011, Sun et al. 2017) and produce recalcitrant litter (Lang et al. 2009), which all play a role in regulating C turnover. Our results suggest that, as a result of this buffering effect, differences in soil nutrient availability, soil and bryosphere microbial communities and broader abiotic properties (e.g. light availability) across contrasting ecosystems (Clemmensen et al. 2015, Jonsson et al. 2015, Jean et al. 2020) may have a minimal effect on how changing precipitation regimes impact C dynamics in moss-dominated forest floors.

Conclusions

Our study demonstrates strong effects of moisture dynamics on the C balance of the bryosphere and upper humus layers, and shows that joint consideration of precipitation volume and frequency is key to understanding moss-dominated forest floor function in boreal regions. This is particularly important as future climate scenarios for boreal and arctic regions predict large changes in moisture regimes through increased precipitation and evapotranspiration, and more frequent extreme precipitation events and droughts (Collins et al. 2013, Berg et al. 2017). Further, our results suggest that the high water holding capacity of the underlying humus layer plays an important role in buffering moss moisture and function against variation in precipitation frequency. Therefore, models of moss C uptake may benefit from accounting for moisture retention and supply from the underlying substrate (Kulmala et al. 2011, Porada et al. 2013). Our findings also indicate that projected increases in the temporal variability of precipitation may have a limited effect on C dynamics of moss-dominated ecosystems as long as precipitation amounts do not decline, at least if environmental conditions that limit ground-level evaporation (e.g. high vascular plant cover, low ground wind speed) persist. Conversely, precipitation regimes leading to drier ground conditions will reduce short-term net C loss both from CO_2 efflux and leaching to deeper horizons. To determine long-term effects of changes in precipitation regime on C dynamics of moss-dominated ecosystems, future work should determine the sensitivity of moss abundance in natural communities to variation in precipitation regimes (Turetsky et al. 2012). Finally, the high degree of buffering of the bryosphere and upper humus layer against environmental variation suggests that drivers of forest floor function such as soil fertility and microbial composition may play only a minor role on C dynamics of moss-dominated ecosystems. Therefore, efforts to predict the response of moss-dominated ecosystems to climate change should also focus on intrinsic properties of the bryosphere and the underlying substrate (e.g. moss species identity, bulk density; Nijp et al. 2014) as these may dominate the response of moss-dominated ecosystems to changing climatic conditions across wide environmental gradients and among ecosystems.

Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.3bk3j9kj4> (Grau-Andrés et al. 2021).

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Author contributions

Roger Grau-Andrés: Conceptualization (supporting); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (lead); Writing-original draft (lead); Writing – review and editing (lead). **David A. Wardle**: Funding acquisition (supporting); Methodology (supporting); Writing – review and editing (equal). **Marie-Charlotte Nilsson**: Funding acquisition (supporting); Methodology (supporting); Writing – review and editing (equal). **Paul Kardol**: Conceptualization (lead); Funding acquisition (lead); Methodology (supporting); Project administration (lead); Resources (lead); Supervision (lead); Writing – review and editing (equal).

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