

REVIEW

Bryophyte-cyanobacteria associations as regulators of the northern latitude carbon balance in response to global change

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Abstract

Ecosystems in the far north, including arctic and boreal biomes, are a globally significant pool of carbon (C). Global change is proposed to influence both C uptake and release in these ecosystems, thereby potentially affecting whether they act as C sources or sinks. Bryophytes (i.e., mosses) serve a variety of key functions in these systems, including their association with nitrogen (N₂)-fixing cyanobacteria, as thermal insulators of the soil, and producers of recalcitrant litter, which have implications for both net primary productivity (NPP) and heterotrophic respiration. While ground-cover bryophytes typically make up a small proportion of the total biomass in northern systems, their combined physical structure and N₂-fixing capabilities facilitate a disproportionately large impact on key processes that control ecosystem C and N cycles. As such, the response of bryophyte-cyanobacteria associations to global change may influence whether and how ecosystem C balances are influenced by global change. Here, we review what is known about their occurrence and N₂-fixing activity, and how bryophyte systems will respond to several key global change factors. We explore the implications these responses may have in determining how global change influences C balances in high northern latitudes.

Keywords: bryophytes, C sequestration, cyanobacteria, heterotrophic respiration, net primary productivity, nitrogen fixation, northern latitude systems

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Introduction

Global change is predicted to affect the net carbon (C) balance of high latitude ecosystems during the next century (Keeling *et al.*, 1996; Magnani *et al.*, 2007). High latitude regions, including boreal forest and arctic ecosystems, cover a large portion of the terrestrial surface area, contain a disproportionately large fraction of the terrestrial C pool, and currently serve as net C sinks (Hayes *et al.*, 2011). Recent measurable increases in air temperature, CO₂ concentrations, nitrogen (N) deposition, and the length of the growing season (Meehl *et al.*, 2007), are predicted to increase the productivity of northern boreal forests and enhance their capacity for C storage (White *et al.*, 2000). Yet, at the same time, observed warmer conditions will enhance decomposition in the belowground subsystem (soil, peat, and other detrital portions of the forest floor), which has been highlighted as a potential global scale positive feedback, increasing the flux of C to the atmosphere and enhancing global warming (Lenton *et al.*, 2008).

Thus, whether these systems continue to serve as net C sinks or become C sources in the future will depend on how both net primary productivity (NPP) and heterotrophic respiration respond to global change factors, notably climate warming, altered precipitation, elevated atmospheric CO₂ and N-deposition rates (Friedlingstein *et al.*, 2006; Schlesinger, 2009).

Predicting whether boreal and arctic ecosystems become net C sinks or net C sources under changing environmental conditions requires focus on the biotic-mediated processes associated with soil C and N cycles, and the linkages between belowground and aboveground subsystems, and C fluxes. Ground covering bryophytes (the bryosphere *sensu* Lindo & Gonzalez, 2010) link above- and belowground processes; they produce highly recalcitrant litter (Lang *et al.*, 2009) and thermally insulate underlying soils, thereby influencing decomposition, and hence both C and N mineralization rates (Startsev *et al.*, 2007). Furthermore, numerous bryophytes in boreal and arctic ecosystems serve as hosts for symbiotic N₂-fixing cyanobacteria, which fix appreciable amounts of N that contribute to stand-level N budgets (DeLuca *et al.*, 2002; Turetsky, 2003) (Table 1). In these high

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Table 1 Rates of bryophyte-associated dinitrogen fixation from published studies in high latitude terrestrial systems. Rates are extrapolated to kg N ha⁻¹ yr⁻¹ where possible for comparison. A full list of references can be found in the Online Supplementary Information

Observed rates (*converted)	Estimated Rate: kg N ha ⁻¹ yr ⁻¹	Ecozone	Location	Reference
ARA $\mu\text{mol m}^{-2} \text{day}^{-1}$				
0.24–2.64	0.01–0.05	High Arctic	Canada	Deslippe <i>et al.</i> (2005)
1–240	0.02–4.5	High Arctic	Norway	Zielke <i>et al.</i> (2005)
511–1308	9.5–24.4	High Arctic lowland	Canada	Chapin <i>et al.</i> (1991)
288	5.4	Low Arctic tundra	Canada	Stewart <i>et al.</i> (2011b)
72–1320*	1.3–24.6	Sub-Arctic	Sweden	Sorensen & Michelsen (2011)
621.6	11.6	Sub-Arctic	Iceland	Henriksson <i>et al.</i> (1987)
ARA $\mu\text{mol g}^{-1} \text{day}^{-1}$				
0–16.6		High Arctic	Sweden	Solheim <i>et al.</i> (1996)
2.4–21.6		Sub-Antarctic	Marion Island	Smith (1984)
0.1–2.0		Boreal forest	Sweden	Gundale <i>et al.</i> (2009)
3.8–22.7*		Boreal forest	Sweden	Gentili <i>et al.</i> (2005)
g N g ⁻¹ moss day ⁻¹				
0.2–2.4		Boreal forest	Sweden	Gundale <i>et al.</i> (2010)
0.3–34.4		Boreal forest	Sweden	Ininbergs <i>et al.</i> (2011)
0.01–0.98		Boreal forest	Sweden	Jackson <i>et al.</i> (2011)
$\mu\text{mol N m}^{-2} \text{day}^{-1}$				
8.16–117.2	0.4–6.6	Sub-Arctic valleys	Sweden	Gavazov <i>et al.</i> (2010)
10.85	0.6	Sub-Arctic	Sweden	Sonesson (1967)
51.49	2.9	Sub-Arctic	Sweden	From: Gavazov <i>et al.</i> (2010)
13.64	0.8	Sub-Arctic	Finland	From: Gavazov <i>et al.</i> (2010)
Rate g N m ⁻² yr ⁻¹				
0.010–0.192	0.1–1.9	Antarctic	Antarctica	Vincent 1988 (In: Cleveland <i>et al.</i> 1999)
0.88*	8.8	Sub-Arctic	Sweden	Sorensen <i>et al.</i> (2006)
0.01–0.35*	0.1–3.5	North Boreal	Sweden	DeLuca <i>et al.</i> (2008)
0.007–0.350	0.1–3.5	Boreal forest	Norway/Finland/Alaska	Van Cleve & Alexander (1981)
0.011–0.049	0.1–0.5	Boreal forest	Global	Cleveland <i>et al.</i> (1999)
0.023–0.193	0.2–1.9	South Boreal	Canada	Markham (2009)
0.49*	4.9	Alpine tundra	Colorado	Bowman <i>et al.</i> (1996)
kg N ha ⁻¹ yr ⁻¹				
0.68	0.68	Low Arctic tundra	Canada	Stewart <i>et al.</i> (2011a)
0.2–7*	0.2–7	North Boreal forest	Sweden	DeLuca <i>et al.</i> (2007)
1.5–2	1.5–2	Boreal forest	Sweden	DeLuca <i>et al.</i> (2002)
0.5–2	0.5–2	Boreal forest	Sweden	Lagerstrom <i>et al.</i> (2007)
0.01–0.9	0.01–0.9	Boreal forest	Sweden	Gundale <i>et al.</i> (2011)
0.4–2	0.4–2	Boreal forest	Sweden	Zackrisson <i>et al.</i> (2004)
1.6	1.6	Boreal forest	Sweden	Zackrisson <i>et al.</i> (2009)
0.5	0.5	Temperate conifer forest	Canada	Lindo & Whiteley (2011)
0.3	0.3	Temperate conifer forest	Canada	Lindo & Whiteley (2011)
0.7–10	0.7–10	Temperate conifer forest	New Zealand	Menge & Hedin (2009)
0.01–0.29	0.01–0.3	Tropical montane forest	Hawaii	Matzek & Vitousek (2003)

*Rates not given in text - estimated from graph.

latitude systems N deposition is low, and bryophyte-cyanobacteria associations often serve as the dominant source of N input. As plant productivity is also often

strongly limited by N, NPP is ultimately dependent on biological N₂-fixation (Tamm, 1991; Vitousek & Howarth, 1991).

Bryophytes have a strong control on key processes involved in determining if ecosystems become C sinks or C sources because they can control both NPP and heterotrophic respiration (DeLucia *et al.*, 2003). While there is a recent increasing appreciation of the role of bryophytes for processes related to ecosystem C balance among some ecologists, the role of bryophytes for understanding ecosystem responses to climate change has been widely overlooked. Here, we propose that changes in bryophyte biomass and productivity under global change factors influence soil C pools through altered input of their litter and their thermal influence on heterotrophic respiration (C release) (Fig. 1). At the same time, these changes in bryophyte biomass combined with alterations in the density and N₂-fixation activity of the cyanobacteria can affect soil N mineralization and availability, and influence NPP (plant C uptake) (Fig. 1). As such, bryophytes and associated cyanobacteria may be key mediators of how boreal and arctic systems respond to global change. In this review we describe what is known about high latitude

bryophyte-cyanobacteria associations, and how global change factors affect the abundance of bryophytes and the N-input of these systems. Finally, we explore several key implications and uncertainties for how changes in bryophyte biomass, productivity, and N₂-fixation activity in response to global change may determine whether high northern latitude systems will serve as C sources or sinks in the future.

The bryophyte-cyanobacteria system

The most widespread and abundant bryophytes in arctic and boreal ecosystems are the pleurocarpous feather mosses (e.g., *Pleurozium schreberi*, *Hylocomium splendens*), and peat mosses (i.e., *Sphagnum* genus) (Turetsky, 2003; Zackrisson *et al.*, 2004; Houle *et al.*, 2006; Lagerström *et al.*, 2007; Stewart *et al.*, 2011b) (Fig. 2). Feather mosses achieve substantial biomass (up to approximately 3 t ha⁻¹: Gundale *et al.*, 2011; Wardle *et al.*, 2012) (Table 2a), and can account for as much as 30% of ecosystem NPP in boreal forest systems (Wardle *et al.*, 2012). In some arctic or peatland ecosystems mosses may account

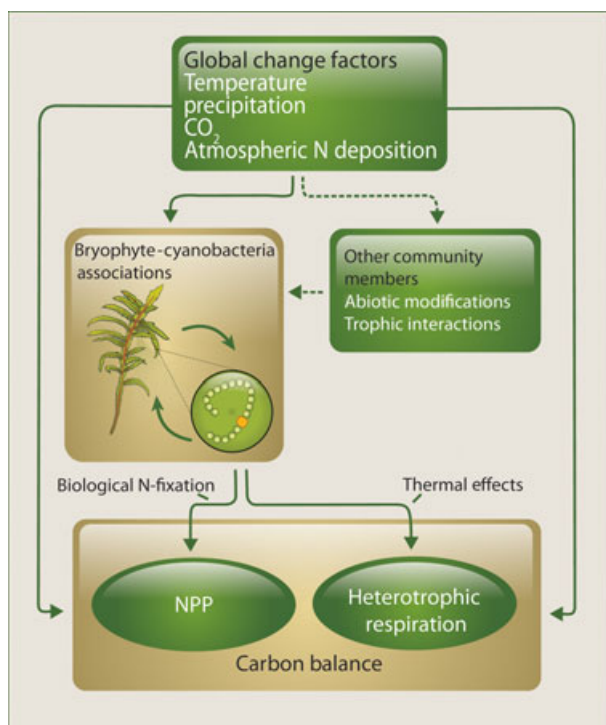


Fig. 1 Whether boreal and arctic systems continue to serve as net C sinks or become C sources in the future will depend on how both net primary productivity (NPP) and heterotrophic respiration respond to a variety of global change factors, notably climate warming, altered precipitation, elevated atmospheric CO₂ and N-deposition rates. Bryophyte-cyanobacteria systems may be key mediators of these responses due to their influence on NPP and heterotrophic respiration.

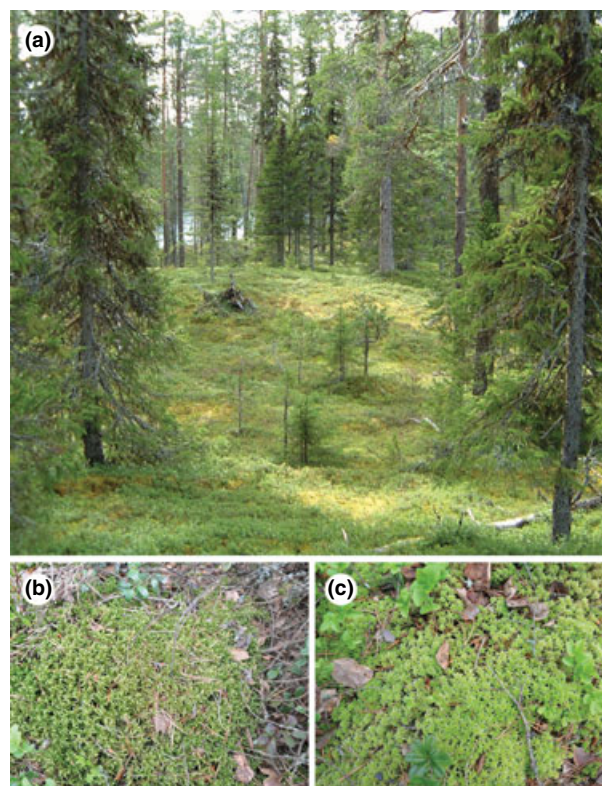


Fig. 2 Ground cover bryophytes can achieve substantial biomass in high latitude systems, such as this boreal forest in Sweden (a). The most widespread and abundant bryophytes in boreal and arctic ecosystems are the pleurocarpous feather mosses [shown is *Pleurozium schreberi* (b)], and members of the peat mosses (*Sphagnum* genus) (c).

Table 2 Bryophyte (feather moss) (a) biomass and (b) net primary productivity (NPP) from published studies in boreal and arctic systems, with single *Sphagnum* citation as reference; other *Sphagnum* studies are covered in several extensive review articles. A full list of references can be found in the Online Supplementary Information

Location	Stand type	Moss type	Biomass	Units	Reference
(a) Moss biomass					
Alaska	Tundra	<i>Pleurozium</i>	70 (approximately)	$\text{g}^{-1}\text{m}^{-2}$	Natali <i>et al.</i> (2012)
Alaska	Black spruce	<i>Pleurozium</i> and <i>Hylocomium</i>	35–101	$\text{g}^{-1}\text{m}^{-2}$	Oechel & Van Cleve (1986)
Alaska	Black spruce	<i>Pleurozium</i>	167	$\text{g}^{-1}\text{m}^{-2}$	Chapin <i>et al.</i> (1987)
Alaska	Black spruce	<i>Hylocomium</i>	112	$\text{g}^{-1}\text{m}^{-2}$	Chapin <i>et al.</i> (1987)
Canada	Black spruce (model)	<i>Sphagnum</i> , <i>Hylocomium</i> , and <i>Pleurozium</i>	46–230	$\text{g}^{-1}\text{m}^{-2}$	Bond-Lamberty & Gower (2007)
Canada	Black spruce	<i>Pleurozium</i> and <i>Hylocomium</i>	200	$\text{gC}^{-1}\text{m}^{-2}$	Harden <i>et al.</i> (1997)
Canada	Black spruce	<i>Pleurozium</i> and <i>Hylocomium</i>	90–420	$\text{gC}^{-1}\text{m}^{-2}$	Harden <i>et al.</i> (1997)
Canada	Jack pine	<i>Pleurozium</i> and <i>Hylocomium</i>	6–20	$\text{gC}^{-1}\text{m}^{-2}$	Vogel & Gower (1998)
Canada	Bog peatland	<i>Pleurozium</i>	207	$\text{g}^{-1}\text{m}^{-2}$	Benscoter & Witt (2007)
Sweden	Boreal forest	<i>Pleurozium</i> and <i>Hylocomium</i>	100–200	$\text{g}^{-1}\text{m}^{-2}$	Wardle <i>et al.</i> (2012)
Sweden	Boreal forest	<i>Pleurozium</i>	250	$\text{g}^{-1}\text{m}^{-2}$	Gundale <i>et al.</i> (2011)
Sweden	Sub-Arctic, birch woodland	<i>Hylocomium</i>	120	$\text{g}^{-1}\text{m}^{-2}$	Callaghan <i>et al.</i> (1978)
Location	Stand type	Moss type	NPP	Units	Reference
(b) Moss NPP					
Alaska	Tundra	<i>Pleurozium</i>	20 (approximately)	$\text{g}^{-1}\text{m}^{-2}\text{yr}^{-1}$	Natali <i>et al.</i> (2011)
Alaska	Black spruce	<i>Pleurozium</i>	64	$\text{g}^{-1}\text{m}^{-2}\text{yr}^{-1}$	Chapin <i>et al.</i> (1987)
Alaska	Black spruce	<i>Hylocomium</i>	37	$\text{g}^{-1}\text{m}^{-2}\text{yr}^{-1}$	Chapin <i>et al.</i> (1987)
Canada	Jack pine	Moss (unspecified)	2–11	$\text{gC}^{-1}\text{m}^{-2}\text{yr}^{-1}$	Vogel & Gower (1998)
Canada	Black spruce	<i>Sphagnum</i> , <i>Hylocomium</i> , and <i>Pleurozium</i>	8–147	$\text{gC}^{-1}\text{m}^{-2}\text{yr}^{-1}$	Bond-Lamberty & Gower (2007)
Canada	Black spruce	<i>Sphagnum</i> , <i>Hylocomium</i> , and <i>Pleurozium</i>	19–114	$\text{gC}^{-1}\text{m}^{-2}\text{yr}^{-1}$	Frockling <i>et al.</i> (1996)
Canada	Black spruce	Feather moss (unspecified)	24	$\text{gC}^{-1}\text{m}^{-2}\text{yr}^{-1}$	Bisbee <i>et al.</i> (2001)
Canada	Black spruce	<i>Pleurozium</i> and <i>Hylocomium</i>	10–30	$\text{gC}^{-1}\text{m}^{-2}\text{yr}^{-1}$	Harden <i>et al.</i> (1997)
Canada	Black spruce	<i>Sphagnum</i>	77	$\text{gC}^{-1}\text{m}^{-2}\text{yr}^{-1}$	Bisbee <i>et al.</i> (2001)
Canada	Boreal peatland	<i>Sphagnum</i> , <i>Hylocomium</i> , and <i>Pleurozium</i>	50 (approximately)	$\text{g}^{-1}\text{m}^{-2}\text{yr}^{-1}$	Camill <i>et al.</i> (2001)
Finland	Norway spruce	<i>Pleurozium</i>	79	$\text{g}^{-1}\text{m}^{-2}\text{yr}^{-1}$	Mäkipää (1995)
Sweden	Sub-Arctic tundra heath	Feather moss (unspecified)	52	$\text{g dwt m}^{-2}\text{yr}^{-1}$	Campioli <i>et al.</i> (2009)
Sweden	Sub-Arctic tundra heath	<i>Pleurozium</i>	162	$\text{g dwt m}^{-2}\text{yr}^{-1*}$	Campioli <i>et al.</i> (2009)
Sweden	Sub-Arctic tundra heath	<i>Hylocomium</i>	38–70	$\text{g dwt m}^{-2}\text{yr}^{-1*}$	Campioli <i>et al.</i> (2009)

*Converted from/d $\times 271$ days.

for nearly 100% of NPP, because vascular plants are scarce (Gunnarsson, 2005). The high estimates of stand-level leaf area index for boreal and peatland mosses (Bond-Lamberty & Gower, 2007) lead to a substantial contribution to energy, water, and CO_2 exchange, and ecosystem productivity in high latitude systems (Table 2b).

Both feather and peat mosses associate with a variety of heterocystous cyanobacteria, primarily within the genera *Nostoc*, *Anabaena*, *Calothrix* and *Stigonema* (Fig. 3) (Gentili *et al.*, 2005; Houle *et al.*, 2006; Ininbergs *et al.*, 2011), which are shown to contribute significantly to stand-level N budgets through the process of dinitrogen (N_2) fixation (DeLuca *et al.*, 2002; Turetsky, 2003). At least some evidence suggests that cyanobacteria

communities can strongly differ between moss species (Opelt *et al.*, 2007; Ininbergs *et al.*, 2011), but it remains largely unknown to what extent the cyanobacteria and moss receive mutual benefit from their association.

Feather and peat mosses offer protective environments for their cyanobionts — some *Sphagnum* species show specialized cells to protect cyanobacteria from the acidic environment (Solheim & Zielke, 2002), while alkaline substances offer protection for epiphytic cyanobacteria (Belnap, 2001). In addition to the hospitable environment that bryophytes provide for cyanobacteria, mutual benefit in the association may occur as a result of metabolite exchange. For instance, the cyanobacteria may provide the bryophyte with N in

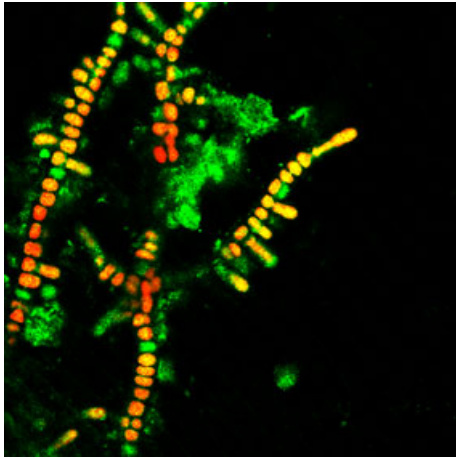


Fig. 3 *Stigonema* on *Pleurozium* leaf (Photo credit: Ewa Mellerowicz). The association between bryophytes and cyanobacteria is thought to be symbiotic, but the extent to which the cyanobacteria and moss gametophytes receive mutual benefit from their association is not yet known.

exchange for C, as shown for *Anthoceros* – a hornwort, in association with the genera *Nostoc* (Meeks & Elhai, 2002). Here, following symbiotic association, cyanobacterial CO₂ fixation is down-regulated while N₂-fixation is stimulated (Adams, 2002; Meeks & Elhai, 2002; Meeks, 2003). At the same time, sugars derived from the host plant compensate the *Nostoc*, and the majority of bioavailable N produced by the cyanobacteria is transferred to the *Anthoceros* (Meeks & Elhai, 2002). These host plants regulate both the production of the motile cyanobacterial stage (hormogonia) required for colonization of new bryophyte cells (Meeks & Elhai, 2002; Adams & Duggan, 2008), and regulate the biomass and N₂-fixation rate of the cyanobacterial colonies (Meeks, 2003). Yet the mechanisms underpinning the cyanobacterial establishment and symbiotic relationship between feather and peat mosses are unknown. Although no specialized structures or transfer cells that would facilitate metabolite exchange have been identified, the exchange of N from the cyanobacteria to moss hosts has been suggested from studies using ¹⁵N₂-labelling or inferred from their ¹⁵N natural abundance values (Hyodo & Wardle, 2009; Gavazov *et al.*, 2010).

Response of bryophyte-cyanobacteria associations to global change factors

Global change factors are well known to alter vascular plant species physiology, distribution, trophic, and competitive interactions within biotic communities; however, only relatively recently has research addressed how global change factors impact bryophyte communities. There is emerging evidence that

bryophyte growth, biomass, and N₂-fixation rates can be highly sensitive to abiotic or biotic changes in terrestrial ecosystems (Solheim & Zielke, 2002; Turetsky *et al.*, 2012). Here, we review the existing literature that is relevant for understanding how global change factors are likely to influence biomass, productivity and N₂-fixing rates of bryophyte-cyanobacteria associations in high latitude ecosystems. We focus primarily on three climate change factors, temperature, precipitation, atmospheric CO₂ concentrations, and one pollution factor, N-deposition. We focus on these four factors because each is frequently cited in the literature as potentially altering ecosystem C balances in boreal or arctic biomes; whereas we do not discuss several additional pollution factors known to impact bryophytes (e.g., heavy metals and sulphur deposition) because they are less frequently proposed to impact biome-scale C balances in these regions (Myking *et al.*, 2009).

Temperature

High latitude ecosystems are predicted to experience the largest magnitude temperature increases during the next century (2–8 °C; Meehl *et al.*, 2007). Some models predict warmer climates and longer growing seasons will result in increased NPP in the high northern latitudes (Friedlingstein *et al.*, 2006; Qian *et al.*, 2010), although it is also recognized that increased NPP may be limited if biological N₂-fixation does not also increase (Hungate *et al.*, 2003; Reich *et al.*, 2006; Jain *et al.*, 2009; Gerber *et al.*, 2010; Zaehle *et al.*, 2010). Biological N₂-fixation is inherently constrained by low temperatures in the high latitudes, due in part to the temperature optimum of the N₂-fixing enzyme nitrogenase, which reaches a maximum efficiency at approximately 25 °C (Vitousek *et al.*, 2002; Houlton *et al.*, 2008), far above mean annual and mean growing season temperatures in high latitude ecosystems (Meehl *et al.*, 2007; Callaghan *et al.*, 2010; Gundale *et al.*, 2012a). Climate warming in northern ecosystems is therefore likely to have a direct positive effect on the N₂-fixation process (Houlton *et al.*, 2008); however, evidence suggests that negative effects of warming on bryophyte productivity and biomass may serve as a stronger control on N₂-fixation per unit area.

Of the relatively few studies investigating the temperature response of bryophyte-cyanobacteria associations in the high latitudes, most have shown that maximal N₂-fixation per unit bryophyte mass are usually achieved between 20 and 30 °C (Chapin *et al.*, 1991; Solheim *et al.*, 2002; Zielke *et al.*, 2002; Gundale *et al.*, 2012a), consistent with the theoretical enzymatic optimum for N₂-fixation (Houlton *et al.*, 2008). Several studies have also shown that temperature responses of

N₂-fixation can be highly species-specific (Gentili *et al.*, 2005; Markham, 2009; Gundale *et al.*, 2012a). In a study focused on two boreal feather moss species, Gundale *et al.* (2012a) showed that an approximately 6 °C temperature increase (from 16.3 to 22.0 °C) caused *Pleurozium schreberi* to achieve between a two- and threefold increase in N₂-fixation rate, whereas N₂-fixation in another feather moss, *Hylocomium splendens*, showed very little response to temperature. The authors speculated that the two feather moss species were associated with different cyanobiont communities (Zackrisson *et al.*, 2009; Ininbergs *et al.*, 2011) with different temperature optima for N₂-fixation, as shown by Gentili *et al.* (2005).

While feather moss N₂-fixation rates per unit mass are likely to increase in response to warming for some species, several studies have shown that the biomass of some mosses decline in response to warming, thereby affecting their N₂-fixation rates. Sorensen *et al.* (2012) showed that 20 years of experimental warming (+3.9 °C) in a subarctic tundra plant community reduced N₂-fixation rates by bryophyte (*Aulacomnium turgidum*) associated cyanobacteria by approximately 50%, which corresponded with a 50% reduction in moss biomass. The authors suggested this response was likely due to increased competition for light and water from vascular plants, which responded positively to warming. Similarly, Lang *et al.* (2012) showed that long-term experimental warming (approximately 2 °C) resulted in near complete loss (i.e., approximately 100% reduction) of non-*Sphagnum* bryophytes in Alaskan arctic landscapes, which corresponded with an increase in vascular plant abundance. These results are further supported by Gundale *et al.* (2012a), who showed that positive temperature response of boreal bryophytes to 6 °C warming were negated when accompanied with a 50% reduction in light. In another study, Bjerke *et al.* (2011) evaluated an alternative mechanism through which climate warming may influence bryophyte abundance, through extreme winter warming events, which can cause reduction in snow pack thickness and increase plant exposure to harsh winter conditions. Using experimental techniques to simulate extreme winter warming events (seven consecutive days above 0 °C), they showed that winter warming had damaging impacts on the feather moss *Hylocomium splendens*, resulting in reductions in photosynthesis and biomass accumulation in the range of 30–40%. Likewise, extreme summer heat events have also been shown to enhance bryophyte mortality. Bragazza (2008) showed that the severe European heat wave during the summer of 2003 resulted in severe desiccation and mortality of hummock forming peat mosses. Collectively, these studies suggest that short-term increases in N₂-fixation

in response to warming may occur due to kinetic responses (Deslippe *et al.*, 2005; Gentili *et al.*, 2005; Gundale *et al.*, 2012a), whereas a majority of studies conducted over longer time scales show that negative impacts associated with warming (i.e., extreme events or more intense vascular plant competition) result in reductions in their biomass, and thus offset or over-ride short term positive effects on N₂-fixation rates. We therefore predict that the long-term effect of increasing temperatures in the far northern latitudes is likely to decrease bryophyte abundance and their N₂-fixation rates on an area basis, but with variable responses expected for different bryophyte species.

Precipitation

As a result of climate warming, precipitation in most high latitude regions is predicted to increase by as much as 30% during the next century; however, in many regions much of this additional precipitation is predicted to occur during the winter months (Meehl *et al.*, 2007). Summer precipitation quantity in the high latitudes may decrease, increase, or remain unchanged depending on the specific region, and in many regions summer precipitation is predicted to occur in larger but less frequent rainfall events (Meehl *et al.*, 2007). Because feather mosses are poikilohydric, many studies have shown that changes in precipitation have great consequences for their abundance and N₂-fixation activity (Zielke *et al.*, 2002, 2005; Gundale *et al.*, 2009, 2012b; Stewart *et al.*, 2011b). In boreal feather mosses, Jackson *et al.* (2011) showed that N₂-fixation nearly doubled in response to a fivefold increase in precipitation quantity, but showed a threefold reduction when precipitation frequency decreased by fivefold. There is, however, some uncertainty regarding whether periodic drought will have lasting impacts on ecosystem N₂-fixation rates. Some studies have suggested that N₂-fixation rates of cyanobacteria may be only temporarily impaired in response to drought events, and that nitrogenase activity can increase within 48–72 h upon bryophyte rewetting (Turkey & Adhikary, 2005). Other studies have shown that recovery from drought can take much longer, on the scale of weeks to months (Gundale *et al.*, 2012b).

While short-term drought events are likely to affect bryophytes and their N₂-fixation activity at a physiological level, long-term reductions in precipitation quantity or frequency are likely to result in reductions in bryophyte abundances within communities. In an arctic landscape in North America, Stewart *et al.* (2011a) showed that moisture was a dominant control of bryophyte abundance (R^2 between 0.33 and 0.63), and that this in turn controlled rates of N₂-fixation per

unit area across different locations. This study is supported by numerous other studies in boreal forest or mire environments showing that the abundance of bryophytes is usually strongly controlled by moisture availability (Hokkanen, 2006; Laitinen *et al.*, 2008). Given that moss moisture status is controlled by the balance between precipitation and evaporative water losses, these studies suggest that the combination of increased vapour pressure deficits associated with climate warming and reduced summer precipitation frequency will have negative impacts on bryophyte growth, biomass, and N₂-fixation activity in arctic and boreal ecosystems (Solheim & Zielke, 2002; Gundale *et al.*, 2012b).

Atmospheric CO₂

There are only limited data to conclude how bryophyte-cyanobacteria associations will respond to elevated CO₂ (Hungate *et al.*, 2004; Reich *et al.*, 2006; Startsev *et al.*, 2007), with a majority of studies focusing on *Sphagnum* growth responses in peatlands. These studies have shown that in the short-term (days or weeks) predicted CO₂ increases for the next century can have neutral or minor positive effects on *Sphagnum* photosynthesis (ranging from 0% to 20% increase) (Jauhiainen & Silvola, 1999; van der Heijden *et al.*, 2000; Toet *et al.*, 2006). In contrast, studies simulating future CO₂ concentrations over longer time scales (i.e., months or years) have shown that bryophyte photosynthesis, growth or biomass responses can be positive (Jauhiainen & Silvola, 1999), neutral (van der Heijden *et al.*, 2000) or negative (Toet *et al.*, 2006; Fenner *et al.*, 2007; Dawes *et al.*, 2011), with changes ranging between approximately -39% to +10% change. For studies showing negative long-term effects, responses were attributed to greater competition with vascular plants for water or light under enriched CO₂ environments.

Whereas a variety of studies have evaluated bryophyte growth responses to elevated CO₂, responses of associated cyanobacteria or N₂-fixation activity have rarely been studied. Several studies from marine environments show that elevated CO₂ concentrations can enhance N₂-fixation by cyanobacteria (Hutchins *et al.*, 2007; Levitan *et al.*, 2007; Sohm *et al.*, 2011), whereas N₂-fixation activity by some terrestrial nodule-forming vascular plants have shown to be impaired by elevated CO₂ (Hungate *et al.*, 2004). In the only study to date looking at bryophyte associated N₂-fixation in response to elevated CO₂ concentrations, Smith (1984) found that simulated future CO₂ concentrations in sub-Antarctic tundra ecosystem depressed rates of N₂-fixation. These studies highlight the paucity of data regarding how the biomass, productivity, and N₂-fixation activity of

bryophyte-cyanobacteria associations will respond to elevated CO₂ concentrations. However, the available data suggest that enhanced CO₂ is likely to have a somewhat smaller effect on bryophytes relative to changes in moisture or temperature, but will likely promote competitive dominance by vascular plants, and thereby contribute to reductions in bryophyte biomass and N₂-fixation rates in many ecosystems (Toet *et al.*, 2006; Dawes *et al.*, 2011).

Atmospheric N-deposition

Human activities have led to a three- to fivefold global increase in anthropogenic N deposition during the last century (Reay *et al.*, 2008), and N-limited northern latitude ecosystems, particularly boreal forests, are proposed to sequester more C in the vegetation and in soils as a result of more N being available to trees (de Vries *et al.*, 2006; Magnani *et al.*, 2007). Numerous studies have shown that bryophyte-cyanobacteria associations can be highly sensitive to anthropogenic N-deposition (Carroll *et al.*, 1999; Bobbink *et al.*, 2010; Sorensen *et al.*, 2012), although responses have also been shown to be highly dependent on deposition rates. Low N-deposition levels (<10 kg N ha⁻¹ yr⁻¹) have been shown to have neutral or negative effects, and rarely positive effects, on bryophyte biomass or productivity in high latitude ecosystems (Bobbink *et al.*, 2010; Gundale *et al.*, 2011; Phoenix *et al.*, 2012). Of the very few studies evaluating how the N₂-fixation activity of bryophyte associations respond to N-deposition, it is clear that cyanobacteria densities on bryophyte leaves and N₂-fixation rates per unit mass or per unit area sharply decline even at extremely low N-deposition rates (Zackrisson *et al.*, 2004; Gundale *et al.*, 2011). Gundale *et al.* (2011) showed that simulated atmospheric N-deposition rates of just 3 kg ha⁻¹ yr⁻¹ resulted in a 50% reduction in N₂-fixation rates on an aerial basis. Bryophytes have also been shown to intercept and sequester a significant fraction of total deposition when levels are low, and thereby limit the uptake of this N by vascular plants (Turetsky, 2003; Forsum *et al.*, 2006; Gundale *et al.*, 2011).

At high N-deposition rates (>10 kg N ha⁻¹ yr⁻¹), numerous studies in a wide range of environments have shown that bryophyte biomass and productivity markedly decline, with complete replacement by vascular plants sometimes occurring (van der Heijden *et al.*, 2000; Heijmans *et al.*, 2001; van der Wal *et al.*, 2005; Nordin *et al.*, 2006; Bobbink *et al.*, 2010). These responses have been attributed to two different mechanisms, including direct toxicity effects of inorganic N ions to bryophyte tissues (van der Heijden *et al.*, 2000), as well as increased shading by vascular plants (van

der Wal *et al.*, 2005). Declines in bryophyte growth and biomass have also been shown to increase the efficiency by which vascular plants acquire atmospheric N-deposition (Gundale *et al.*, 2011). This occurs because when bryophyte biomass is reduced, less N is sequestered into their tissues, and a larger proportion of the total N input enters the soil directly as inorganic N, which is then more easily acquired by vascular plant roots compared to N bound in bryophyte tissues (Lang *et al.*, 2009).

Given the different effects of low vs. high rates of N-deposition on bryophytes reported in the literature, understanding the impacts of atmospheric N-deposition on bryophytes in arctic or boreal ecosystems requires evaluation of actual deposition rates in these systems. Gundale *et al.* (2011) showed that a majority of the land surface area in boreal forests (>70%) currently receives N-deposition rates of 3 kg N ha⁻¹ yr⁻¹ or less, with land area in excess of these levels primarily occurring in the boreal portions of Europe (i.e., Sweden, Finland, western Russia). Likewise, almost the entire arctic region receives N-deposition rates well below 3 kg N ha⁻¹ yr⁻¹ (Dentener *et al.*, 2006). These actual N-deposition rates are far below the levels used in a majority of experiments or field studies showing significant bryophyte declines, and therefore suggest that bryophyte biomass or productivity are unlikely to be significantly affected by current N-deposition levels in most of the area in boreal or arctic regions; whereas, the literature suggests that reductions in associated cyanobacteria densities and N₂-fixation activity are likely to occur at these levels (Zackrisson *et al.*, 2009; Gundale *et al.*, 2011; Ackermann *et al.*, 2012).

Competitive and trophic controls

Global change factors are likely to affect other biotic components of the high latitude communities, which in turn may exert indirect control on bryophyte-cyanobacteria associations. As described above, a variety of studies have suggested that in the long-term positive responses of vascular plants to warmer temperatures, elevated CO₂, or atmospheric N-deposition usually have negative consequences for the biomass or N₂-fixation activity of bryophyte-cyanobacteria associations (van der Wal *et al.*, 2005; Toet *et al.*, 2006; Fenner *et al.*, 2007; Dawes *et al.*, 2011; Sorensen & Michelsen, 2011; Lang *et al.*, 2012). For most of these studies negative effects on bryophytes were attributed to reductions in moisture or light availability as a consequence of enhanced vascular plant growth. Yet not all interactions between bryophytes and vascular plants are negative; studies have also shown that some vascular plant species can interact positively with bryophytes (Gornall

et al., 2009, 2011). Using a 16-year species removal experiment in a boreal forest, Gundale *et al.* (2010) showed that several slow growing late successional dwarf shrub species (*Vaccinium vitis-idaea*, *Empetrum hermaphroditum*) had positive effects on bryophyte biomass and growth. However, bryophyte interactions with early successional, faster growing deciduous species were usually negative (Gundale *et al.*, 2010, 2012c), as consistent with numerous other studies (van der Wal *et al.*, 2005; Olofsson, 2006; Gornall *et al.*, 2007). Functional shifts in vascular plant communities in response to global change have been shown to be a common phenomenon (van der Wal *et al.*, 2005), whereby vascular plant species with higher relative growth rates (i.e., less nutrient conserving) replace slower growing species (e.g., Nilsson *et al.*, 2002; Strengbom *et al.*, 2003; Bokhorst *et al.*, 2009). As such, positive interactions between bryophytes and slow growing vascular plant species are likely to weaken, whereas competitive interactions with fast growing species, such as grasses, are likely to strengthen in response to global change, and therefore have negative consequences for growth and biomass of mosses.

In addition to plant competitive controls on bryophyte-cyanobacteria associations, a variety of studies have shown that trophic interactions can influence the biomass of bryophytes-cyanobacteria associations. Bryophyte grazers include a wide array of mammalian, avian, and microfauna (e.g., micro-arthropods) species, with studies on the latter grazer group remaining extremely rare (Lindo & Gonzalez, 2010). In general, bryophytes are not very palatable or nutritious; however, in some northern latitude ecosystems, notably the arctic, they are commonly consumed by geese (*Anser*, *Branta*, and *Chen*), lemmings (*Lemmus*), reindeer (*Rangifer tarandus*), and muskox (*Ovibos*), which can directly reduce bryophyte biomass (van der Wal & Brooker, 2004; Gornall *et al.*, 2009). Climate change, along with various other factors, may increase the abundance of some herbivores (e.g., geese) in arctic and boreal landscapes (Jefferies & Rockwell, 2002; McLaren *et al.*, 2004; Ims *et al.*, 2007), whereas some other species (e.g., reindeer) may show region specific responses (Kausrud *et al.*, 2008; Hansen *et al.*, 2011). While there remains substantial uncertainty in how herbivory will change as a result of climate change in arctic or boreal landscapes, these studies suggest that global change factors may alter the intensity of interactions between herbivores and bryophytes (Gornall *et al.*, 2009; Sjögersten *et al.*, 2012).

In addition to direct consumption, there are several other mechanisms through which herbivores may influence bryophyte biomass (Gornall *et al.*, 2009). For instance, a variety of studies have shown that the

bryophyte layer can be severely disturbed through trampling by large ungulates (van der Wal & Brooker, 2004), or through digging and tunnelling activity of smaller animals (e.g., geese and lemmings) (Gornall *et al.*, 2009). Another pathway through which mammalian or avian herbivores can negatively impact bryophytes is through dung and urine inputs, whereby nutrient cycling rates and availability in the soil is enhanced (van der Wal & Brooker, 2004). While bryophytes are likely to absorb a majority of nutrients when dung and urine inputs are low (Sjögersten *et al.*, 2010), high levels of dung and urine are likely to eventually enhance nutrient availability to vascular plants and promote faster growing species, such as graminoids (van der Wal & Brooker, 2004; Olofsson, 2006). These studies indicate that increased herbivore pressure can often result in reductions in the biomass of bryophytes and other cryptogams, usually corresponding with an increased abundance of fast growing vascular plant species (Gornall *et al.*, 2009; Gough *et al.*, 2012). Only a few exceptions have shown that herbivores can increase the abundance of mosses (Hansen *et al.*, 2007) or increase the dominance of other functional groups, such as lichens (*Stereocaulon* sp.) (van der Wal *et al.*, 2001).

Influence of bryophytes on arctic and boreal ecosystem C balance

Ecosystem C stocks are controlled by the balance of C inputs, described as NPP, and C losses that primarily occur through heterotrophic respiration. Here, we discuss how bryophyte-cyanobacteria associations are likely to influence both NPP and heterotrophic respiration, and further describe their role in coupling these two processes together as the bryophyte-cyanobacteria system responds to global change.

Net primary productivity (NPP)

While bryophyte-cyanobacteria associations serve as the dominant biological N-input through atmospheric N_2 -fixation, vascular plants account for a majority of productivity in many high latitude ecosystems; therefore, a key process that NPP in these systems depends on is the transfer of N from bryophyte-cyanobacteria associations to vascular plants. Yet, it is currently unclear what the 'fate' of newly fixed N is, and through which pathway and what timescale it becomes available to vascular plants. Here, we consider three pathways, which operate at different spatial and temporal scales, through which N from the bryophyte-cyanobacteria system is transferred to vascular plants (Fig. 4), and the consequences for how NPP may respond to global change. The first potential pathway is that

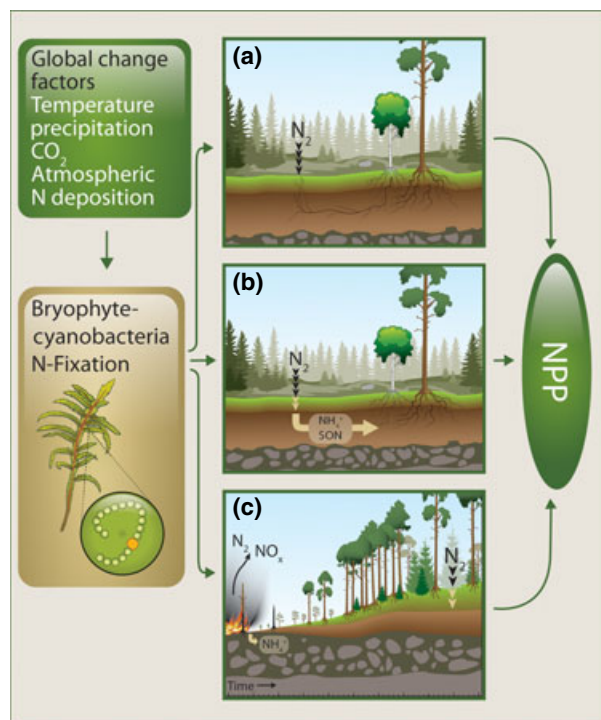


Fig. 4 Three ecosystem-level pathways for N fixed by bryophyte-associated cyanobacteria to reach vascular plants. (a) Immediate, direct pathway whereby vascular plants acquire N via mycorrhizae that pilfer N from living or recently dead organic matter. (b) Intermediate scale pathway through which N is released from decomposing bryophyte litter. (c) Organic N accumulated in humus is released quickly and in large amounts during fire events; the majority of which is lost to the atmosphere, and a small portion of which becomes available as inorganic N.

vascular plants directly obtain N from the living moss system, through parasitic or mutualistic mycorrhizal linkages (Fig. 4a). Parke & Linderman (1979) observed that mycorrhizal fungi associated with vascular plants colonized moss stems and leaves, and surmised that vascular plants may pilfer N from living bryophyte-cyanobacterial association through their mycorrhizae. Subsequently, numerous studies have observed ectomycorrhizal fungi present in both green and senescent moss tissue, and suggest that a transfer of nutrients occurs between the moss system and trees (Carleton & Read, 1991; Kauserud *et al.*, 2008; Davey *et al.*, 2009, 2012). Using a long-term boreal fire chronosequence, Hyodo & Wardle (2009) showed that in old forests where nutrient mineralization and availability are low, and N_2 -fixation rates are high, vascular plant and feather moss $\delta^{15}N$ values converged near zero (i.e., the theoretical $\delta^{15}N$ value of newly fixed N), suggesting that the dwarf shrub community that dominates in late-successional communities may directly take up recently

assimilated N from feather mosses before isotope fractionation occurs (i.e., during litter decomposition). These studies suggest that mutualistic or parasitic relationships likely exist between some vascular plant species and bryophyte-cyanobacteria associations that may result in direct N-transfer to the vascular plants. In this scenario, immediate feedbacks between the bryosphere and vascular plants are facilitated through a tightly coupled system, and thus vascular plant NPP could be highly responsive to changes in bryophyte-cyanobacteria N₂-fixation activity.

Evidence that mosses retain a majority of newly fixed N (Hyodo & Wardle, 2009; Gavazov *et al.*, 2010) suggests that changes in N₂-fixation rates may in the short run impact bryophyte productivity and biomass. It also suggests at intermediate temporal scales, moss-derived N enters the soil as bryophyte litter, and becomes available to vascular plants through decomposition processes (Fig. 4b). As mosses are highly recalcitrant, N-release from decomposing bryophytes is relatively slow, thus this pathway would transpire over a time scale of years to decades. In addition, the high C : N quality of bryophyte litter generates a strong immobilizing environment that results in a high degree of competition for N between plants and microbes (McFarland *et al.*, 2010), thereby potentially limiting N availability to vascular plants.

In boreal forests, and to a much lesser extent in arctic ecosystems, fire serves as an additional pathway through which N is transferred from bryophytes to vascular plants (Fig. 4c) over decadal to century time scales. In this pathway, both the bryophyte and humus soil layers are consumed during fire, causing a substantial loss of N capital that has accumulated in moss, vascular plant, and humus to the atmosphere (Bormann *et al.*, 2008). This large reduction in total N capital corresponds with a large increase in soil inorganic N concentrations which are more easily obtained by vascular plants (Fig. 4c). Plants that tolerate or rapidly colonize following fire are able to acquire this inorganic N pulse, resulting in an increase in labile litter production, and more rapid circulation of this N between vegetation and soil (Wardle *et al.*, 2012). Yet moss and cyanobacteria recolonization is slow following fire, and lower N₂-fixation rates may persist for many decades (Zackrisson *et al.*, 2004; DeLuca *et al.*, 2008) resulting in no new N entering the system.

Which of these three N transfer pathways predominates has implications for how responsive vascular plant NPP will be to changes in bryophyte cover and N₂-fixation rates as climate change occurs. If vascular plant communities directly acquire bryophyte N from living bryophyte tissues via mycorrhizal linkages (Carleton & Read, 1991; Kausarud *et al.*, 2008; Davey

et al., 2009, 2012), NPP is likely to be highly sensitive to changes in bryophyte-cyanobacteria N₂-fixation rates. In contrast, if vascular plants primarily acquire N from decomposing bryophyte litter, or over centennial time scales via the fire-cycle, increases or decreases in N₂-fixation rates in response to global change factors may have little immediate consequence for vascular plant NPP. Instead, indirect control of NPP may occur through bryophyte influence on belowground C and N cycles.

Heterotrophic C losses and ecosystem C balances

While contributing to aboveground biomass, mosses are intricately linked with the belowground soil system through their production of low quality litter and their insulating effects on soil (Lindo & Gonzalez, 2010; Turetsky *et al.*, 2010). Decomposition processes, and thus heterotrophic C losses, are governed by temperature, moisture and litter quality entering the soil. Decomposition rates of bryophyte tissues have consistently been shown to be slower compared to most vascular plants species (Wardle *et al.*, 2003; Cornelissen *et al.*, 2007; Lang *et al.*, 2009). For example, using a 21 week experimental incubation approach, Hobbie (1996) showed that two bryophyte species in the Alaska tundra, *H. splendens* and *S. balticum*, showed substantially lower litter respiration and mass loss rates relative to most vascular plants in the system. Likewise, Wardle *et al.* (2003) showed that feather mosses decomposed between 10% and 40% slower than a diverse group of vascular plant species in a Swedish boreal forest. In a subarctic community, Dorrepaal *et al.* (2005) showed that *Sphagnum* decomposed between three- and fivefold slower than an array of vascular plants over an 8 month incubation period. Furthermore, Lang *et al.* (2009) showed that a wide array of bryophyte species on average decomposed approximately fivefold slower than the vascular plants in the same system.

Bryophytes also form thick carpets in boreal and arctic environments that can influence soil temperature regimes that further slows decomposition (Sharratt, 1997; Gornall *et al.*, 2007; Blok *et al.*, 2011). A variety of studies have shown that soil temperature during the growing season is negatively correlated with moss depth (Olofsson *et al.*, 2004; van der Wal & Brooker, 2004; Gornall *et al.*, 2007; Cannone & Guglielmin, 2009). For instance, Gornall *et al.* (2007) showed in arctic tundra that soil temperatures beneath thin (3 cm) relative to thick (12 cm) moss mats were in the range of 2–3 °C warmer during the summer months, achieved 4 °C higher maximum temperatures, and showed greater diurnal and annual temperature fluxuations. A variety of studies using experimental moss removal approaches

have provided further evidence of the strong influence mosses have on soil temperature (Luthin & Guymon, 1974; Startsev *et al.*, 2007; Blok *et al.*, 2011). Startsev *et al.* (2007) showed that removal of the feather moss layer in a Canadian boreal forest resulted in a 21% increase in soil temperatures at 5-cm depth during unfrozen portion of the year, and also increased the daily and annual temperature amplitudes. Likewise, Blok *et al.* (2011) showed that moss removal in a Siberian tundra community resulted in an 11% increase in heat transfer to the soil during the growing season, an impact that has been linked to permafrost stability in far northern latitude regions (Luthin & Guymon, 1974; Matthews *et al.*, 1997; van der Wal & Brooker, 2004).

Given that the processes of C and N mineralization are directly linked to one another, low decomposition rates associated with the presence of bryophyte cover simultaneously causes N availability to vascular plants to decrease and soil C to accumulate (Gorham, 1991; Malmer *et al.*, 2003; Gornall *et al.*, 2007; Turetsky *et al.*, 2010; Wardle *et al.*, 2012). This relationship between bryophytes, soil processes, and vascular plants therefore serves as a key feedback in high latitude ecosystems that inversely couples aboveground and belowground C pools in response to climate change. When abiotic or biotic factors are present to promote moss growth and biomass, they fix N₂ while simultaneously slowing soil C and N mineralization, causing soil C and N to accumulate, and aboveground NPP to decrease (van der Wal & Brooker, 2004; Gornall *et al.*, 2007; Wardle *et al.*, 2012). In contrast, when biotic or abiotic change factors reduce moss biomass, soil C and N mineralization accelerate, usually increasing the abundance of relatively fast growing vascular plants (van der Wal *et al.*, 2005; Toet *et al.*, 2006; Dawes *et al.*, 2011; Lang *et al.*, 2012), and potentially decreasing soil C as soils warm and receive more labile litter inputs.

Given the emerging evidence that bryophytes serve as regulators of C balances in response to global change, biogeochemical and climate models focused on ecosystem C balances in boreal and arctic ecosystems have started to explicitly consider the functional role of bryophytes, and have further demonstrated their impacts on ecosystem C balances. Earlier models demonstrated the importance and impact of bryophyte cover on soil moisture and temperature. Beringer *et al.* (2001) demonstrated how mosses insulated and protected soil layers producing cooler summer temperatures and warmer winter temperatures, as well as greater storage of belowground moisture compared to bare soil. Other models have demonstrated that the presence of bryophytes significantly alters predicted changes of NPP, N mineralization, and aboveground and belowground C stocks in response to climate

change. For example, Zhuang *et al.* (2002) modelled the effect of bryophyte cover reduction following fire disturbance, and showed substantial losses in belowground C stocks, even after aboveground C stocks recovered. Recently, simulations of climate alterations from process-based models by Turetsky *et al.* (2012) demonstrated how a 30% increase in climate drying (either through increased evapotranspiration under warming and/or decreased precipitation) in a boreal system could result in a 20% net reduction in total ecosystem C through reduced peat accumulation. Although the predicted changes were manifest over long time scales, the authors emphasized the need to incorporate moss-dominated landscapes into process and systems-based climate change models. These modelling studies corroborate the role of bryophytes in regulating ecosystem C balances in boreal and arctic ecosystems.

Conclusions

It is clear that bryophyte-cyanobacteria associations carry out several key functions in boreal and arctic N-limited ecosystems through their production of recalcitrant litter, thermal protection of soils, and role as the primary source of N through biological N₂-fixation. It is also clear that global change factors are likely to influence their biomass, productivity, and N₂-fixation activity. For almost all experimental studies evaluating the response of bryophyte biomass, productivity or N₂-fixation activity over multi-year time scales in response to three climate change factors (climate warming, reduced summer precipitation frequency, and elevated CO₂), a common pattern that emerges is that bryophytes are usually impaired, whereas vascular plants with relatively high growth rates are often enhanced. It is also clear that high levels of N-deposition can have detrimental impacts on bryophytes; however, because rates of N-deposition are so low in boreal and arctic ecosystems, the ability of bryophytes to sequester N into their tissues at these levels likely plays a key role in preventing community or ecosystem level impacts from occurring. As our review describes, there is strong support in the scientific literature that reductions in bryophyte biomass are likely to impact C dynamics in these ecosystems, by increasing heterotrophic C losses, and often enhancing NPP through increases in fast growing vascular plant species. These empirical studies are increasingly corroborated by process-based modelling approaches that show the presence or absence of bryophytes can strongly influence the net C balances of these ecosystems.

Despite these advances, many aspects of the role that bryophyte-cyanobacteria associations play in regulating

ecosystem responses to global change require further investigation. For instance, there is a notable lack of studies addressing their response to long-term increases in elevated CO₂, as well as interactive effects between environmental change factors. In addition, while the literature shows that indirect community interactions, such as herbivory, are likely to be a key pathway through which bryophytes respond to climate change, uncertainty remains in whether global change factors will cause these interactions to strengthen or weaken. Understanding how N derived from bryophyte cyanobacteria N₂-fixation is transferred to non-N₂-fixing plants, and over what time-scales this occurs, is an additional frontier that is key for determining how sensitive NPP will be to global change.

The knowledge about how bryophytes link above-ground and belowground processes is useful for developing governmental policy aimed at sequestering C. For instance, ecosystem management approaches aimed at enhancing C sequestration by increasing NPP, such as fertilization programs, are becoming more common in boreal forests. Unintended negative effects of these programs on bryophytes may inevitably result in offsetting losses of soil C that minimize the effectiveness of such programs to sequester C. Likewise, land use changes, such as afforestation programs or large herbivore management decisions may have unintended negative effects on C sequestration in these regions due to their antagonistic interactions with bryophytes (but see Freeman *et al.*, 2012). A detailed understanding of these relationships may help facilitate more accurate predictive modelling of how boreal and arctic ecosystem C dynamics will influence the global C cycle, which is highly relevant for an array of policy, globally, that is based on climate change modelling.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. References.

Data S2. References.