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 predicted 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 (N$_2$)-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 N$_2$-fixing capabilities facilitate a disproportionally 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 N$_2$-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, CO$_2$ 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 CO$_2$ 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 N$_2$-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
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 N\textsubscript{2}-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](image1.png)

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 CO\(_2\) 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](image2.png)

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).
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 CO2 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 (N2) 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 alkaline 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
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 wave 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 (R² 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...
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 N\(_2\)-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 CO\(_2\), or atmospheric N-deposition usually have negative consequences for the biomass or N\(_2\)-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 (Jefferyes & 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 N₂-fxation, 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 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 surmized 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 N₂-fxation rates are high, vascular plant and feather moss δ¹⁵N values converged near zero (i.e., the theoretical δ¹⁵N value of newly fxed 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 the bryophyte and humus to the atmosphere (Bormann et al., 2010; Lindo & Gonzalez, 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 & Guglielmino, 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 fluctuations. 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 recalci-trant 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 CO$_2$ 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 aboveground 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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