



## Tansley review

# The resilience and functional role of moss in boreal and arctic ecosystems

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## Summary

Mosses in northern ecosystems are ubiquitous components of plant communities, and strongly influence nutrient, carbon and water cycling. We use literature review, synthesis and model simulations to explore the role of mosses in ecological stability and resilience. Moss community responses to disturbance showed all possible responses (increases, decreases, no change) within most disturbance categories. Simulations from two process-based models suggest that northern ecosystems would need to experience extreme perturbation before mosses were eliminated. But simulations with two other models suggest that loss of moss will reduce soil carbon accumulation primarily by influencing decomposition rates and soil nitrogen availability. It seems clear that mosses need to be incorporated into models as one or more plant functional types, but more empirical work is needed to determine how to best aggregate species. We highlight several issues that have not been adequately explored in moss communities, such as functional redundancy and singularity, relationships between response and effect traits, and parameter vs conceptual uncertainty in models. Mosses play an important role in several ecosystem processes that play out over centuries – permafrost formation and thaw, peat accumulation, development of microtopography – and there is a need for studies that increase our understanding of slow, long-term dynamical processes.

## I. Mosses in the northern, high-latitude region

Many northern, high-latitude ecosystems are characterized by an abundance of mosses. In general, mosses and other nonvascular plants show a pattern of increasing abundance with increasing latitude, whereas vascular plant species richness declines steeply along the same gradient (Vitt & Pakarinen, 1977; Wielgolaski *et al.*, 1981; Jägerbrand *et al.*, 2006). At a landscape scale, moss diversity is highest in mesic, high-pH habitats and on particular substrates such as fallen logs (Robinson *et al.*, 1989; Belland & Schofield, 1994; Vitt *et al.*, 2003; Mills & Macdonald, 2004; Hylander & Dynesius, 2006). Despite their abundance, only in the past few decades have mosses been recognized as important, dynamic components of northern plant communities. In part, this is likely because many mosses are difficult to identify to species, which could cause ecologists to focus on other components of vegetation or lump species into groups that may or may not be meaningful. Mosses also are more difficult to use in glasshouse or common-garden experiments than vascular plants, and thus have not been used as common model systems for ecological research (but see Jonsson & Söderström, 1988; Rixen & Mulder, 2005; Lindo & Gonzalez, 2010). For many decades, bryophytes were regarded as slow-growing and evolutionarily rigid plants that exhibited little adaptive change in response to recent climatic and environmental variation. However, it is now recognized that bryophytes display a variety of life history strategies, can have polymorphism comparable to vascular plants, and can form relatively large populations in environments subject to change and fine-scale disturbance (Slack, 1982; Longton, 1988; Vitt, 1990; Okland, 1995; Pharo & Zartman, 2007).

In general, mosses possess several key traits that allow them to persist in cold regions, including a high degree of phenotypic plasticity and a broad response of net assimilation rates to temperature. Mosses can be regarded as opportunistic in terms of CO<sub>2</sub> exchange in that they are able to respond positively to favorable environmental conditions where and when they occur, with CO<sub>2</sub> assimilation even during low temperature and irradiance (Kallio & Heinonen, 1975; Oechel & Sveinbjörnsson, 1978; Harley *et al.*, 1989). Key functional traits include tolerance to desiccation and the ability to switch quickly between metabolic activity and rest. While vascular plants avoid desiccation during drought by actively regulating internal water content (i.e. homoiohydry) through morphological adaptations such as well-developed conducting systems, leaf stomata, cuticle, and roots, these features are all poorly developed or absent in mosses. Instead, mosses tolerate periods of drought largely through physiological responses, such as by suspending metabolism (controlled cessation) when water is not available and by withstanding cell desiccation.

In their Tansley review, Proctor & Tuba (2002) argued that the moss strategy of poikilohydry 'is not merely the primitive starting point of plants that failed to achieve homoiohydry, but a highly evolved strategy of adaptation in its own right, optimal in some situations and at least a viable alternative in some others'. When faced with desiccation, net assimilation rates in mosses usually decline rapidly as tissue water content falls below the

threshold required to maintain full turgor (Longton, 1988). Their cytoplasm can survive at low water contents for long periods, and upon rehydration resume metabolic activity. This strategy, however, has metabolic costs, as recovery is preceded by a burst of respiration that results in a net energy loss (Skre & Oechel, 1981). Desiccation time affects the timing and completeness of recovery, and extended desiccation can cause intense respiration and death. While many moss species can tolerate desiccation, there is a wide variety of adaptations in terms of water economy among mosses (Vitt & Glime, 1984), as well as large variation in the relation of desiccation tolerance to desiccation intensity (Proctor & Tuba, 2002).

In general, these traits are not considered to be specific adaptations to cold region environments, but almost certainly increase the fitness of mosses growing in harsh northern conditions. In turn, and as described in more detail in Section II, moss traits related to water, nutrient, and thermal tolerances influence ecosystem processes such as net primary productivity (NPP), decomposition, and soil energy fluxes and thus are important for our understanding of how northern ecosystems respond to perturbation following disturbance.

The goal of this review is to investigate the role of mosses in the stability and resilience of northern ecosystems to disturbance. While stability emphasizes equilibrium and resistance to change, ecological resilience is defined as the ability of a system to absorb perturbations while retaining the same basic structure and ways of functioning. Resilience thus reflects the capacity of a system to adapt to stress and change (Holling, 1973; Gunderson, 2000). Understanding the resilience of northern communities and ecosystems is important given that recent warming has resulted in changes in sea ice, snow cover, glaciers and permafrost (cf. Hinzman *et al.*, 2005; Grosse *et al.*, 2011; Karlsson *et al.*, 2011; Liston & Hiemstra, 2011), and has increased the frequency and intensity of wildfires and insect outbreaks (Soja *et al.*, 2007; Kurz *et al.*, 2008; Mack *et al.*, 2011; Turetsky *et al.*, 2011). Cumulatively, these changes have the potential to greatly influence plant species composition, abundance, and diversity, with implications for ecosystem function and feedbacks to regional and global climate (cf. Euskirchen *et al.*, 2007, 2009).

Boreal and arctic ecosystems may differ in their response to disturbances, including climate change. Boreal forests are generally dominated by a few common tree species, often with a single species dominating large areas. This may increase the vulnerability of boreal ecosystems and landscapes to disturbance, including pulse (short-term events that impact a system rapidly such as wildfire or rapid permafrost degradation) or press (impacts driven by decadal to century-scale changes such as soil warming and top-down permafrost thaw) disturbances (Grosse *et al.*, 2011). On the other hand, boreal forests are strongly regulated by and adapted to disturbance. Boreal fire intervals range from c. 50 to 500 yr depending on climate and soil drainage conditions, and many species exhibit traits that enable post-fire persistence (cf. Pausas *et al.*, 2004; Johnstone, 2006). Insect outbreaks, ranging from chronic to epidemic, also are typical of the boreal disturbance regime (Soja *et al.*, 2007). Relative to boreal forests, arctic plant communities may be less adapted to recovery

following disturbance. Typical fire return intervals in the Low Arctic, which is dominated by shrub tundra, are *c.* 140–480 yr (Higuera *et al.*, 2011). Further north, biomass is lower and fire rarely occurs, with the fire return interval as high as 5000 yr (Hu *et al.*, 2010). However, if perturbed during disturbance, the long life span of some arctic plants through clonal reproduction may allow for rapid recovery (Chapin *et al.*, 1994).

Here, we use literature review, synthesis of empirical studies and model simulations to explore issues related to the role of northern mosses in ecological resilience. We focus only on mosses, and do not consider other nonvascular groups such as liverworts or hornworts, although some of our findings may be relevant to these other plant types.

## II. The role of moss in ecological resilience

### 1. The effects of moss on northern ecosystem function

Several reviews have assessed the role of mosses in food web dynamics, plant competition, and carbon and nutrient cycling (cf. Van Breemen, 1995; Turetsky, 2003; Nilsson & Wardle, 2005; Cornelissen *et al.*, 2007; Lindo & Gonzalez, 2010; Turetsky *et al.*, 2010). Mosses can dominate primary productivity in northern environments, on average contributing to 20 and 50% of above-ground NPP in boreal forests and wetlands, respectively (Turetsky *et al.*, 2010). Mosses are important for nitrogen cycling and availability for vascular plant uptake because of their low nitrogen-use efficiency, high cation exchange (leading to nitrogen interception and retention), and slow decomposition rates (cf. Hobbie *et al.*, 2000; Malmer *et al.*, 2003; Turetsky *et al.*, 2010). By regulating soil temperature and moisture, mosses also control concentrations of plant-available nitrogen (cf. Gornall *et al.*, 2007). Additionally, some species, particularly feather mosses and *Sphagnum*, can serve as an important source of ecosystem nitrogen by facilitating biological nitrogen fixation (Basilier, 1979; DeLuca *et al.*, 2007; Markham, 2009; Kip *et al.*, 2011). Mosses are also important to phosphorus cycling in that they absorb phosphate and reduce availability for vascular uptake (Chapin *et al.*, 1987). On the other hand, Crowley & Bedford (2011) found that moss created more oxidized conditions in shallow fen soils, and overall enabled greater phosphorus acquisition by forb species. This highlights the fact that mosses can have positive or negative interactions with vascular plants, depending on species and abiotic conditions. Gornall *et al.* (2011) present a conceptual model of the impacts of the moss layer on vascular performance in which negative effects begin to outweigh any positive effects with increasing depth of the moss layer.

Because of their influence on soil climate, NPP, nutrient content, and decomposition rates, mosses facilitate surface peat accumulation and thus long-term soil carbon accumulation. As a result of slow rates of soil carbon accumulation over millennia, large stocks of carbon are currently held in frozen mineral soils and in frozen and unfrozen peatland soils, all of which may be vulnerable to soil warming and changing disturbance regimes (Grosse *et al.*, 2011). Based on *c.* 620 peat cores collected across western

Canada (Zoltai *et al.*, 2000), bryophytes (mostly *Sphagnum* remains) were estimated to represent *c.* 50% of the total peat volume (Turetsky, 2003). In model simulations of > 8000 yr of peat accumulation, vascular plants accounted for 65% of total NPP but only 35% of the remaining peat mass. Vascular plants had < 5% of their total NPP remaining in the peat, whereas moss groups had > 10% remaining (Frolking *et al.*, 2010).

By regulating soil climate and peat accumulation, mosses strongly influence vascular plant recruitment and regeneration. Because organic soils tend to be poor seedbeds, in particular for broadleaf species that have small seeds, mosses indirectly control vascular regeneration (cf. Johnstone & Chapin, 2006; Astrup *et al.*, 2008; Camill *et al.*, 2010; Soudzilovskaia *et al.*, 2011). Mosses also appear to directly inhibit vascular plant germination through allelopathy (cf. Steijlen *et al.*, 1995), although Soudzilovskaia *et al.* (2011) found strong negative relationships between bryophyte phenolics and seedling germination in the laboratory but not in field settings. Decreases in moss abundance and resulting decreases in soil moisture can reduce habitat quality for wildlife in some cases (Hodson *et al.*, 2010). In general, mosses play an integral role in northern ecosystem food webs, because they are eaten by some animals (Prins, 1982), regulate key habitat conditions such as soil climate, and serve as important habitat for soil organisms that interact to form the detrital food web (Lindo & Gonzalez, 2010).

Mosses and peat play an important role in permafrost stability by buffering surface soils and permafrost from fluctuating air temperatures. In the growing season, surface soil temperatures are negatively related to the thickness of organic soil layers (Harden *et al.*, 2006; Romanovsky *et al.*, 2008). Both observational and manipulative studies have quantified the importance of mosses to ground heat flux (van der Wal & Brooker, 2004; Gornall *et al.*, 2007; Blok *et al.*, 2011). Also, modeling studies incorporating thick organic soils have shown its importance in permafrost dynamics (e.g. Yi *et al.*, 2007; Lawrence *et al.*, 2008; Wisser *et al.*, 2011). While some moss species have high moisture retention, in general the porosities of organic soil layers are higher than mineral soils (Yi *et al.*, 2009). Thus, drainage occurs with seasonal ice thaw and the ensuing drier conditions further protect surface permafrost.

Mosses also are important to the formation of microtopography – elevated mounds (hummocks) separated by low hollows – in both forests and peatlands. Hummocks tend to vary in height from a few cm to 1 m (Ivanov, 1981). Paleoecological and modeling evidence suggests that these microtopography features are long-lived (e.g. Nungesser, 2003). The formation of hummock-hollow microtopography creates a gradient of distance to water table, increasing the diversity of microhabitats and niches for moss species. Hummock species must be able to retain and use water efficiently and avoid desiccation, more so than species living in hollows (Titus *et al.*, 1983; Rydin, 1993). For example, species in the *Sphagnum* section *Acutifolia* form dense populations of small individuals, leading to greater water retention and transport than hollow communities. *Sphagnum* communities in hollows are often dominated by species in the section *Cuspidata*, which tend to have larger capitula diameters and

lower population densities. Because of such traits, hollow species are highly productive but prone to desiccation, and thus are competitively excluded from hummocks (Rydin, 1993). Several studies have documented substantial variation in decomposition rates among dominant *Sphagnum* spp., generally with slower decomposition rates in hummock than in hollow species (Johnson & Damman, 1991; Turetsky *et al.*, 2008; Lang *et al.*, 2009b; but see Hogg, 1993; Turetsky *et al.*, 2010). The biochemical mechanism leading to differential decomposition rates is not well understood but appears to be related to nitrogen (cf. Lang *et al.*, 2009b) and/or structural carbohydrates such as sphagnum (cf. Turetsky *et al.*, 2008; Hájek *et al.*, 2011). Regardless of the mechanism, differences in decomposition rates between hummock and hollow mosses are thought to affect peat properties and hydraulic transmissivity over time, reinforcing moisture differences among microhabitats (cf. Nungesser, 2003; Belyea & Baird, 2006).

By influencing the diversity of habitats for moss species, microtopography increases the diversity of functional traits related, in particular, to water balance. This in turn increases resistance at an ecosystem scale to drought as well as wildfire (Benscoter & Wieder, 2003; Belyea & Baird, 2006). Despite being situated further from the water table, hummocks burn less frequently and severely than hollows in continental forests and peatlands. This is because high water retention by hummock mosses inhibits both the initiation and downward propagation of combustion (Benscoter *et al.*, 2011). Across *c.* 80 black spruce forests in Alaska, the area of unburned *Sphagnum* hummocks was a strong predictor of how much organic soil escaped burning at a stand scale (Shetler *et al.*, 2008). *In situ* survival within these unburned 'islands' could also be important to recolonization and rates of succession post-fire. Hylander & Johnson (2010) documented that small-scale refugia can be important for forest bryophytes after fire, but concluded that their role in recolonization is not well understood.

## 2. Using models to explore the role of moss in ecological resilience

Because of the already-mentioned difficulty of using mosses in plant-level experiments, and the cost and difficulty of performing field experiments in remote northern areas, ecological models are an important tool for understanding the function and resilience of mosses. The strong role of moss in both fast (cf. soil heat fluxes) and slow (cf. permafrost aggradation, peat accumulation) ecosystem dynamics means that models are sometimes the only available tool, given their ability to examine vegetation and ecosystem responses over long time-frames. On the other hand, model results are fundamentally circumscribed by what pools and processes are actually built into the model and how they are represented, and model results can never be perfectly confirmed (Oreskes *et al.*, 1994). Despite these limitations, model simulations are critical to identify knowledge gaps, formulate hypotheses, and examine long-term dynamics. In this way, empirical studies will continue to inform modelling work, and vice versa.

Dynamic vegetation models (DVMs) represent a synthesis of research in four main groups of processes: plant geography, plant physiology and biogeochemistry, vegetation dynamics, and biophysics. The most important unique feature of DVMs is their ability to simulate vegetation dynamics, that is, transient changes in vegetation structure in response to variations in the external environment. DVMs generally simulate the effects of changes in climate on natural vegetation in a spatially explicit manner. Within a grid cell, vegetation may be modeled by fractions or strata occupied by multiple plant functional types (PFTs). Competition among PFTs is considered for basic resources, including light, nitrogen, and water. Vegetation growth in DVMs is represented by NPP, which is usually modeled explicitly as the balance of carbon uptake by photosynthesis and release by autotrophic respiration. Plant succession processes, such as establishment, competition, and mortality, are often included.

Plant functional types are plant species grouped according to their effects on community or ecosystem function (Chapin *et al.*, 1998; Walker *et al.*, 1999), how they respond to disturbance (Friedel *et al.*, 1988; Smith *et al.*, 1997), and/or similarities in resource use (Grime, 1979). PFT classification is central to DVMs, yet the sets of PFTs adopted by existing models can be arbitrary and the appropriate parameter values for particular PFTs are sometimes not well established (but see Kattge *et al.*, 2011). This is particularly true for mosses – given that bryophyte species are often lumped into a single PFT in models or not included at all. A number of DVMs and ecosystem models have included moss as a single or as multiple PFTs (e.g. Pastor *et al.*, 2002; Nungesser, 2003; Zhuang *et al.*, 2006; Bond-Lamberty *et al.*, 2007; Yurova *et al.*, 2007; Heijmans *et al.*, 2008; Euskirchen *et al.*, 2009; Wania *et al.*, 2009; Froliking *et al.*, 2010). These models vary in time step as well as how moss is parameterized (Table 1). In empirical studies, mosses are often analyzed as groups according to substrate preference (e.g. rock vs log; Frisvoll & Presto, 1997; Astrom *et al.*, 2007), overstory canopy preference (Astrom *et al.*, 2007; Baldwin & Bradfield, 2007), and microtopographic position, all of which reflect the response of mosses to moisture, light, and chemical gradients (cf. Robinson *et al.*, 1989; Glaser *et al.*, 1990; Bridgman *et al.*, 1996). Quantifying variation in traits related to drought tolerance and avoidance (such as stem density, leaf/branch morphology, water retention and capillary wicking, metabolic change following re-wetting), light acquisition and tolerance (such as leaf area, chlorophyll content, pigmentation), and nitrogen use and economy (such as nitrogen-use efficiency, affiliation with N<sub>2</sub> fixers, cation exchange capacity) would allow for more robust classification of response traits (Lavorel & Garnier, 2002; Waite & Sack, 2010).

There is surprisingly little information directly linking moss traits to specific ecosystem functions (effect traits, Suding *et al.*, 2008; but see Cornelissen *et al.*, 2007; Waite & Sack, 2011). Studies have commonly grouped mosses by life history traits such as spore size, frequency of sporophyte production, growth form, and presence of vegetative reproduction (cf. During, 1992; Baldwin & Bradfield, 2007; Dorell & Cronberg, 2011). Some studies have related moss life history traits to water retention and



**Table 1** Comparison of characteristics (related to moss PFTs) of the models as they were used in this paper

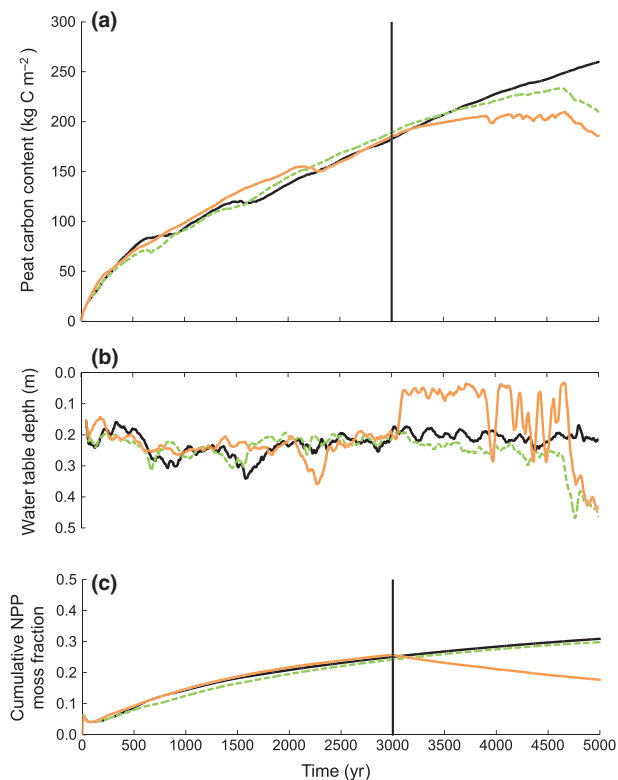
Model	Moss PFTs	Controls on moss NPP	Moss PFT parameters	Competition with vascular PFTs	Time Step/ Duration	Reference
Biome-BGC	One – feather moss or <i>Sphagnum</i> depending on dominant moss type	Temperature, water content, [CO <sub>2</sub> ], nutrients, light	Water: carbon at full turgor Fraction external water Leaf water potential at full and zero turgor Reduction in conductance as a result of cuticular water	Water, light, nutrients	Daily time step for seasons to decades	Bond-Lamberty <i>et al.</i> (2007)
TEM-DVM	Two – <i>Sphagnum</i> and feather moss, which were parameterized depending on the ecosystem type in which they are located	Temperature, water content, [CO <sub>2</sub> ], nutrients, light	Parameterized and calibrated with PFT-specific: GPP NPP Maximum potential NPP Nitrogen uptake Nitrogen availability Net nitrogen mineralization Vegetation C and N Soil C and N	Light, nutrients	Monthly time step for seasons to decades	Euskirchen <i>et al.</i> (2009)
HPM	Five – brown moss, three <i>Sphagnum</i> (lawn, hummock, hollow), feather moss	Water table depth, peat depth (as proxy for nutrients)	Optimum water table and peat depth NPP response to suboptimal conditions Maximum potential NPP Initial litter decomposition rate	Not directly; inferred from PFT realized niches in water table and peat depth	Annual time step for decades to millennia	Frolking <i>et al.</i> (2010)

GPP, gross primary productivity; NPP, net primary productivity; PFT, plant functional type.  
STM-TEM does not include PFTs and is therefore not included here.

economy (e.g. Hedderson & Longton, 1996). Chapin *et al.* (1996)'s classification of arctic plant species first partitioned cryptogam species into moss and lichen, and then further divided mosses into *Sphagnum* vs non-*Sphagnum* spp. based on properties related to peat accumulation. Segregating *Polytrichum* spp. from other moss species also has been suggested based on life history and water economy traits (cf. Gordon *et al.*, 2001). Elumeeva *et al.* (2011) quantified water retention across 22 bryophyte species at both the shoot and colony levels, and their analyses provided support for six PFTs based on water economy and habitat preference. Studies that screen moss species for a variety of traits will be useful for PFT classification, but linking traits to ecosystem processes is necessary (Suding *et al.*, 2008).

Frolking *et al.* (2010) used relationships between relative NPP, water table depth and peat height to represent five moss PFTs in the Holocene Peat Model (HPM), a one-dimensional model that simulates peat accumulation at an annual time step as the net balance between above- and below-ground productivity and litter

or peat decomposition. In a new simulation using the HPM, we explored the role of moss in the response of peat accumulation to a drying perturbation. We imposed climatic drying as a linear increase in evapotranspiration (ET) starting 3000 yr after the beginning of the simulation and ending with a 30% increase by the end of the 5000 yr simulation. We then conducted the same drying simulation, this time completely removing the moss cover at the onset of drying and increasing vascular NPP so that total NPP was essentially unchanged. The baseline 5000 yr simulation represents a typical raised bog, where the transition between the fen and bog phases occurs after *c.* 1500 yr, and where the vegetation cover of the last 3500 yr comprises primarily *Sphagnum* mosses and shrubs. Gradual drying reduced peat accumulation, though the effect was small for the first 1500 yr of drying, by which time ET had declined by 23%. After this, once a threshold was reached where the loss of water through ET was too high to be compensated by precipitation, the system responded with a relatively abrupt drop in water table and a period of net peat loss.



**Fig. 1** Holocene Peat Model (HPM) simulations of: (a) accumulating peat carbon over the 5000 yr simulation for the baseline scenario (solid black line), a gradual drying starting in simulation year 3000 (dashed green line), and removal of moss and drying starting in year 3000 (solid orange line); (b) 50 yr simple moving window average of simulated water table depth for the three scenarios; and (c) moss fraction of cumulative total net primary productivity (NPP). The parameterization of the model is similar to the one presented in Frohling *et al.* (2010) for the Mer Bleue peatland (45.40°N, 75.50°W), a 28 km<sup>2</sup> ombrotrophic bog. The prescribed annual precipitation input is based on a regional precipitation reconstruction (Muller *et al.*, 2003) corresponding to the first 5000 yr of peat accumulation of the Mer Bleue peatland, including random variability based on the confidence intervals of the reconstruction (variability during 0–3000 yr is caused only by stochastic precipitation).

In the ‘drying + no moss’ scenario, C accumulation slowed earlier (by *c.* 500 yr) in the period of declining ET, leading to wetter conditions as the peat could not outgrow the water table. At the same time the deeper peat is relatively unaffected, as it resists drying because of its low hydraulic transmissivity. When the simulated water table is near the surface, it responds to dry periods (low precipitation generated stochastically) with much greater variability (Fig. 1). Across the no disturbance, drying, and drying + no moss scenarios, the total accumulated peat mass was 260, 210, and 186 kg C m<sup>-2</sup>, respectively (of which 136, 103 and 64 kg C m<sup>-2</sup> were derived from moss litter). In these HPM simulations, moss presence maintained two ecosystem characteristics – carbon accumulation rate, and water table depth along with its associated vegetation composition – for much longer in the face of a slowly but persistently increasing ‘press’ disturbance (drying).

Simulations with another process-based model, the soil thermal model (STM) version of the Terrestrial Ecosystem Model

(STM-TEM), have also explored the importance of moss in the resilience of carbon and nutrient cycling in boreal conifer forests following wildfire. Zhuang *et al.* (2002) compared recovery of soil moisture, temperature, and aspects of nutrient cycling in scenarios with and without moss recovery post-fire. For several decades after fire, soils in the burned stand are warmer and drier than in the unburned stand because more radiation reaches the soil surface, causing higher evaporation, and because of greater drainage associated with a thicker active layer after fire (Fig. 2a,b). During ecosystem recovery post-fire, the simulation with moss growth resulted in both lower NPP (Fig. 2d) and heterotrophic respiration (Fig. 2e) in comparison to the simulation without moss growth. Although the presence of mosses had little effect on the pattern of NEP after fire (Fig. 2f), it did affect the patterns of accumulation of carbon in the ecosystem, as vegetation carbon accumulation is greater in the simulation without moss growth (Fig. 2g) because of greater nitrogen uptake in warmer soils, and soil carbon accumulation is slightly greater in the simulation with moss growth (Fig. 2h), because of slower decomposition in colder soils. Thus, these simulations indicate that mosses play a role in the resilience of soil carbon recovery after fire in the ecosystem.

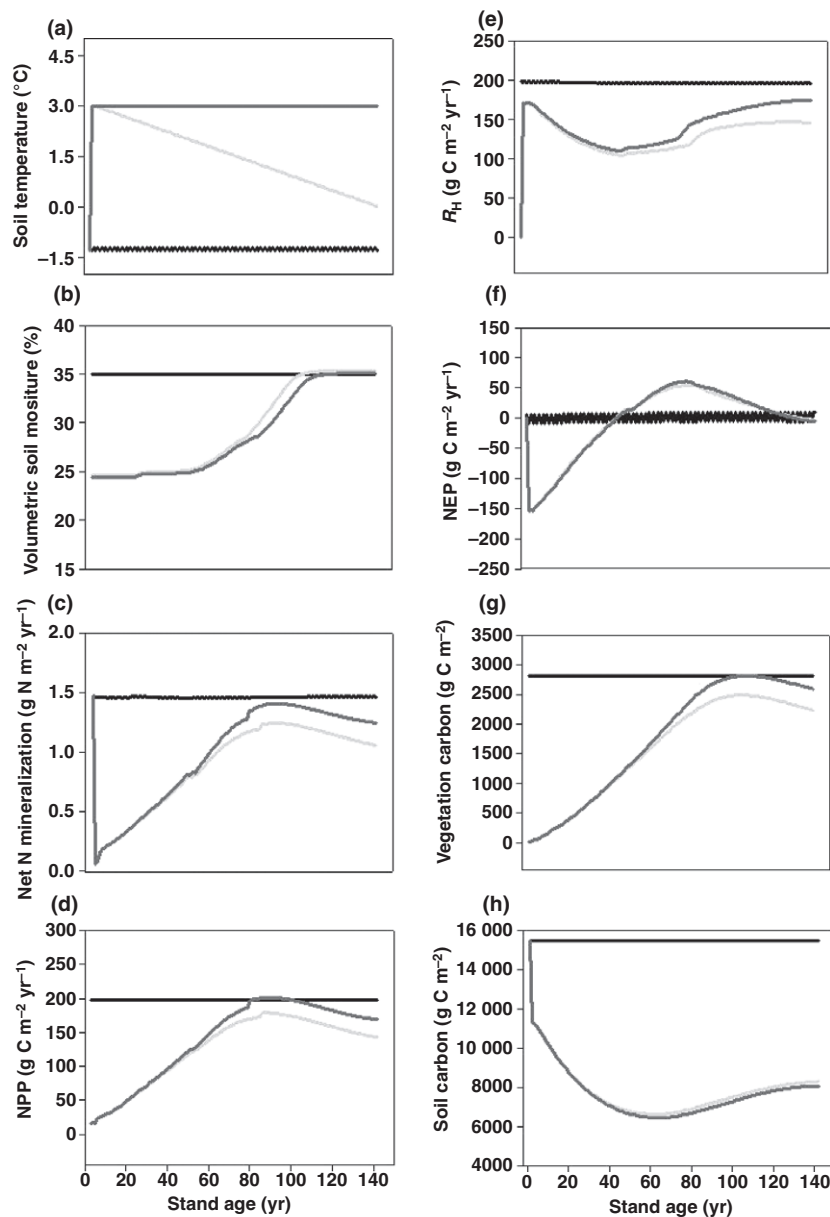
The HPM and STM-TEM simulations show that loss of the ground moss layer can have important consequences for how ecosystem processes either resist or respond to perturbations associated with drying and wildfire. Both simulations considered the effects of large reductions in moss abundance and did not consider how changing moss species composition might influence ecosystem processes following disturbances. While some severe disturbances, such as prolonged drought or severe burning, may reduce total moss abundance, in many cases, changing environmental conditions are more likely to cause shifts in moss species composition. To our knowledge, no empirical or modeling study has systematically varied the relative abundance of individual moss PFTs within a community to ask questions about the effects of moss abundance vs composition on ecosystem processes. In Section III, we explore how northern moss abundance and composition likely will respond to climate change and disturbances, and how this could influence the recovery of ecosystem processes.

### III. Response of moss to disturbance

In a ‘stable state’, ecosystem attributes may fluctuate, but within limits maintained by internal ecosystem structures or external constraints (Scheffer *et al.*, 2001). As a result, ecosystems undergoing successional compositional changes are not necessarily changing state (Drever *et al.*, 2006). Disturbance and succession are linked because disturbance is often a mechanism for resetting succession, renewing limiting resources, and allowing species to coexist (Glenn-Lewin & Van Der Maarel, 1992).

#### 1. Directional autogenic and exogenic succession

In northern peatlands, primary succession has been determined by stratigraphical reconstruction of plant macrofossils with depth in peat cores or using spatial time-since-initiation



**Fig. 2** Soil thermal model version of the Terrestrial Ecosystem Model (STM-TEM) simulations of the dynamics of soil temperature, soil moisture, nitrogen cycling, carbon fluxes, and carbon stocks in the sensitivity analysis for moss growth. Scenarios include a stand with moss cover that was not burned (black line), a stand that was burned and moss allowed to grow during stand development (also known as the 'standard' scenario, light gray line), and a stand that was burned and moss not allowed to grow during stand development (dark gray line). (a) Soil temperature integrated over 20 cm of soil relative to the soil surface; (b) mean volumetric soil moisture of the humic organic layer from May to September; (c) annual net nitrogen mineralization; (d) annual net primary productivity (NPP); (e) annual heterotrophic respiration/decomposition ( $R_H$ ); (f) annual net ecosystem production (NEP); (g) vegetation carbon; (h) soil carbon. Reprinted, with permission, from Zhuang *et al.* (2002).

chronosequences. These studies in general show directional succession where peat initiation coincides with minerotrophic swamp and fen communities, which develop into ombrotrophic bog communities. The transition from minerotrophic to ombrotrophic conditions is driven by the accumulation of a peat layer that insulates the peatland surface from water inputs from underlying mineral soil and surrounding areas, leading to changes in pore water chemistry such as decreases in calcium and magnesium concentrations and increases in acidity (Gignac & Vitt, 1990). While brown mosses such as *Warnstorfia* spp. are often

the first mosses to dominate during peatland succession, subsequent colonization of *Sphagnum* spp. is a critical point in peatland succession. Some *Sphagnum* spp. accelerate rates of peat accumulation because of their poor litter quality that resists decomposition (e.g. Turetsky *et al.*, 2007; Straková *et al.*, 2010). The high cation exchange capacity of *Sphagnum* has previously been linked to rapid acidification associated with *Sphagnum* expansion (Clymo & Hayward, 1982; Van Breemen, 1995), which, in turn, favors ombrotrophic *Sphagnum* spp. and limits the growth of other plant species (Rydin *et al.*, 1999). Recently

the acidification mechanism via differences in cation exchange capacity has been questioned, because no differences were found between brown mosses and *Sphagna* (Soudzilovskaia *et al.*, 2010). Instead, Soudzilovskaia *et al.* (2010) suggested that the rapid acidification results purely from the accelerated height growth that prevents the neutralizing flow of mineral-rich water into the surface (Soudzilovskaia *et al.*, 2010). While the development of ombrotrophy is considered to be a gradual process (Korhola, 1992), paleoecological records often show a rapid transition to ombrotrophic plant assemblages (Janssens *et al.*, 1992; Hughes & Barber, 2003). Disturbance such as severe burning also can favor *Sphagnum* and cause rapid ecosystem shifts to a bog stage (Tuittila *et al.*, 2007; Tahvanainen, 2011). Alternatively, in some cases, directional succession towards ombrotrophic conditions can be reversed as a result of changes in hydrology or the loss of peat with increased decomposition, which favors establishment of fen vegetation (Tolonen, 1971; Hughes & Dumayne-Peaty, 2002).

Mosses also undergo strong directional succession during post-fire recovery. While succession of the vascular understory community in boreal forests can follow initial floristics, with the post-fire community consisting largely of species found in unburned mature forests (Foster, 1985), mosses often follow relay floristics (Foster, 1985; Benscoter & Vitt, 2008). Soon after fire in boreal forests and peatlands, pioneer moss species such as *Polytrichum piliferum* and *Polytrichum juniperinum* may temporarily replace late successional mosses *Dicranum polysetum*, *Hylocomium splendens*, *Ptilidium ciliare* and *Pleurozium shreberi* (Maikawa & Kershaw, 1976; Marozas *et al.*, 2007). In continental bogs, *Sphagnum* communities tend to dominate midsuccessional sites, but are outcompeted by feather mosses with canopy closure (Benscoter & Vitt, 2008).

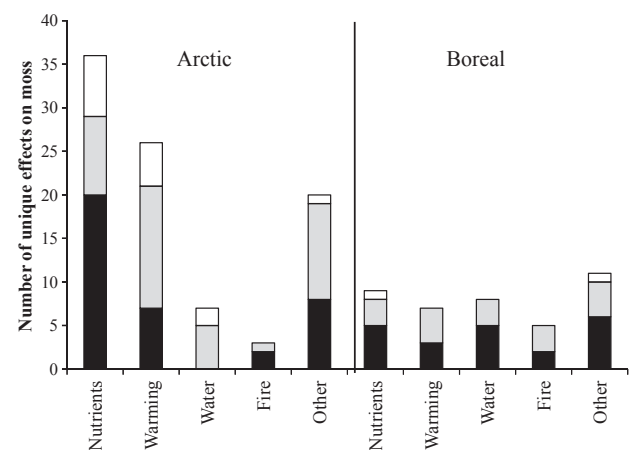
Independent of fire, *Sphagnum* spp. can actually displace feather moss communities in more mesic forests, likely by increasing soil moisture and thus reducing canopy cover, leading to peat formation through paludification (Fenton & Bergeron, 2006). In such conditions, tree growth is reduced (Sarkkola *et al.*, 2003) but *Sphagnum* mosses are protected from the stress induced by strong irradiation (Hájek *et al.*, 2009). Such humid microclimates created by *Sphagnum* and tree canopy favor epiphytic mosses and lichens, leading to increased ecosystem diversity (Kuusinen, 1996).

## 2. Moss community response to disturbance

Floristic composition is often used as a measure of ecological resilience following some disturbance event. Lack of convergence to predisturbance floristic composition does not necessarily imply a lack of resilience with respect to other ecosystem characteristics. For example, despite shifts in species composition, an ecosystem could still be ecologically resilient if there was still recovery back to a similarly functional forest, peatland, or tundra ecosystem. However, given the importance of mosses to the numerous ecosystem processes reviewed earlier, it seems likely that substantial changes in moss abundance and/or community composition will have implications for how ecosystems function (see also Figs 1, 2). We used a literature review to examine responses across

disturbance types (i.e. fire, warming, nutrient addition, drought) and ecosystems (tundra, meadow, forest, peatland). We included studies that examined moss community responses to disturbance as the change in total species richness, total abundance (% cover of moss), and/or net growth rates. We also noted where studies quantified changes in functional composition. Because studies reported different response variables, we did not perform a formal meta-analysis but instead summarized qualitative trends. In particular, we were interested in whether various disturbances caused significant decreases, increases, or no net change to the moss community, and whether this varied by biome or ecosystem type (see the details in Supporting Information Table S1).

We compared moss community responses across disturbance types between boreal and arctic ecosystems. In boreal communities, mosses declined in abundance or species richness in *c.* 50% of cases, while in arctic communities mosses declined in 40% of cases (Fig. 3). These trends do not appear to be affected by the duration of study. Of the studies that examined moss recovery



**Fig. 3** Results of a literature review of moss community responses (increase, white; no change, gray; decrease, black) to disturbance as changes in total moss % cover (abundance), species richness, and/or productivity. Results from different ecosystem types (forests vs wetlands) or from unique sites contained in a single study are included as unique effects. Studies used in the compilation of Fig. 3 are listed below. Also see Supporting Information Table S1 for additional details and results from each study. Arnesen (1999); Arroniz-Crespo *et al.* (2011); Astrom *et al.* (2005, 2007); Baldwin & Bradfield (2010); Botting & Fredeen (2006); Breeuwer *et al.* (2009); Chapin *et al.* (1995); Dorrepaal *et al.* (2004); Dynesius & Hylander (2007); Dynesius *et al.* (2009); Gerdol *et al.* (2007); Gordon *et al.* (2001); Graglia *et al.* (2001); Grellmann (2002); Gunnarsson & Rydin (2000); Gunnarsson *et al.* (2004); Hauessler *et al.* (2002, 2004); Heijmans *et al.* (2002); Hobbie & Chapin (1998); Hobbie *et al.* (1999); Hotes *et al.* (2010); Hunt *et al.* (2005); Jagerbrand *et al.* (2006); Jandt *et al.* (2008); Jonasson (1992); Jonasson *et al.* (1999); Jorgenson *et al.* (2010); Juutinen *et al.* (2010); Kelley & Epstein (2009); Kemper & Macdonald (2009); Keuper *et al.* (2011); Kreyling *et al.* (2008); Lang *et al.* (2011); Mack *et al.* (2008); Marozas *et al.* (2007); Molau & Alatalo (1998); Murray *et al.* (1993); Newmaster & Bell (2002); Newmaster *et al.* (1999); Nilsson *et al.* (2002); Phoenix *et al.* (2001); Potter *et al.* (1995); Press *et al.* (1998); Racine *et al.* (2004); Richardson *et al.* (2002); Riutta *et al.* (2007); Rixen & Mulder (2005); Robinson *et al.* (1998); Rudolphi & Gustafsson (2011); Rydgren *et al.* (2004); Saarnio *et al.* (2003); Shaver *et al.* (2001); Söderström (1988); Sonesson *et al.* (1996, 2002); Speed *et al.* (2010); van der Wal *et al.* (2005); Wardle *et al.* (2008); Weltzin *et al.* (2000, 2001, 2003); Wiedermann *et al.* (2007).



for > 10 yr, mosses still showed declines in total cover or species richness in c. 45% of cases (Table S1). However, within most disturbance types, there was considerable variation in the responses – positive, negative, neutral – of both boreal and arctic mosses, and this variation did not decline with increasing sample size.

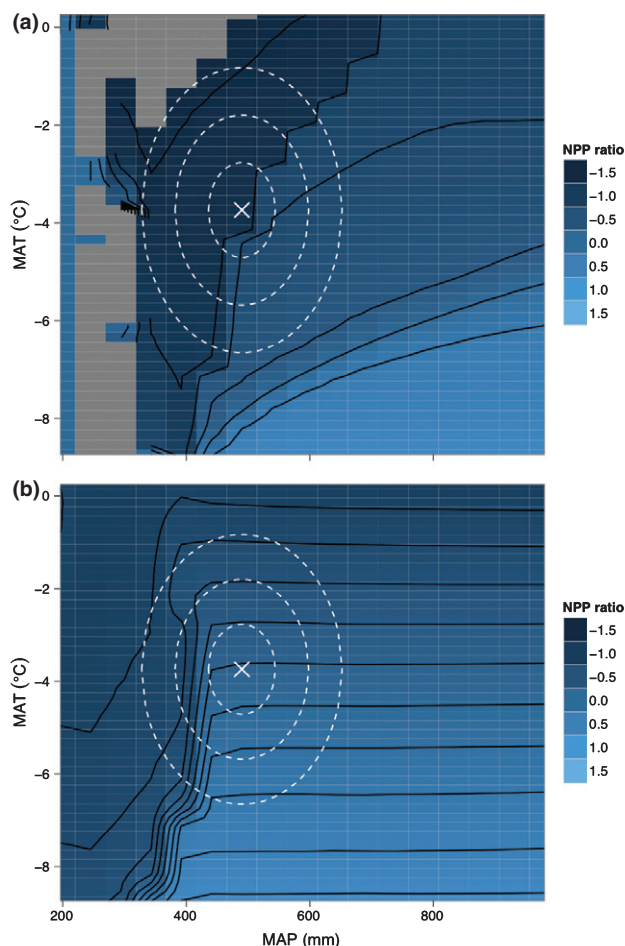
At least partly because of differences in disturbance severity, moss communities may be more resistant (exhibit greater stability) to disturbance in wetter environments (sheltered microhabitats, north-facing sites, riparian forests, wetlands, etc.) than in drier habitats. In response to timber harvest practices, boreal mosses are more resistant to perturbation in north-facing slopes and riparian forests than in drier forests (Astrom *et al.*, 2007; Dynesius *et al.*, 2009; Baldwin & Bradfield, 2010), likely as a result of changes in both microclimate and microhabitats following harvesting. For example, clear cuts in north-facing stands in western Canada were shadier than south-facing clear cuts, which promoted moss survival (Astrom *et al.*, 2007). However, Baldwin & Bradfield (2010) found that disturbance-associated species also persisted longer during vegetation recovery in drier forests than in more humid forests. Perhaps similarly, *Sphagnum* mosses appear to be more resistant to change during warming than other mosses (Gunnarsson, 2005; Lang *et al.*, 2009a,b, 2011). The persistence of *Sphagnum* mosses, which tend to be found in wetter microhabitats and promote soil moisture retention, also increased the stability of the entire plant community to warming (Keuper *et al.*, 2011; Lang *et al.*, 2011). However, following severe disturbances, *Sphagnum* may have low resilience. For example, while bryophyte abundance recovered more quickly from disturbance related to seismic exploration in riparian tundra than in drier tundra, *Sphagnum* cover showed low resilience (Jorgenson *et al.*, 2010).

The majority of studies included in our synthesis quantified changes in moss abundance and/or components of diversity, and for simplicity we considered all of these variables together. While it is clear from our review that there are ample studies of moss community change following disturbance, there are far fewer studies investigating linkages between plant community change and recovery of ecosystem processes. Clearly, changes in moss abundance and diversity may not have identical impacts on ecosystem-level processes. Change in total abundance of the moss ground layer, for example, is relevant for some ecosystem processes, such as water retention and energy fluxes (cf. Blok *et al.*, 2011), but the effects of species richness are less clear. An understanding of how species composition responds to disturbance also can reveal important insights into community or ecosystem function, as communities with no net change in total moss abundance or species richness may still be undergoing significant shifts in species or functional group composition. Not surprisingly, in our synthesis, several studies found post-disturbance increases in *Polytrichum* spp. at the expense of species such as *Tomenthypnum nitens* and feather mosses (Jonasson, 1992; Potter *et al.*, 1995; Botting & Fredeen, 2006). This is not necessarily indicative of low resilience, unless community composition remains altered or the ecosystem is pushed into new successional trajectories.

### 3. Effects of warming on moss–vascular plant relations

Air temperature increases indirectly affect moss communities by altering vascular plant biomass, affecting light intensities for ground layer mosses, and stimulating nutrient turnover. Enhanced nutrient mineralization as a result of warming are expected to favor fast-growing species over slower-growing species with conservative nutrient-use strategies such as some mosses. The shading hypothesis predicts that increased nitrogen mineralization and availability with warming will favor vascular productivity more than moss productivity, and that increased shading by the vascular plant canopy will reduce moss fitness (cf. van der Wal *et al.*, 2005). On the other hand, the race for space hypothesis (following Keuper *et al.*, 2011) predicts that warming will stimulate moss productivity, which in turn stimulates vascular vertical incremental growth (i.e. grow or be buried by moss). Our literature review showed that boreal and arctic moss communities have variable responses to warming experiments (see Fig. 3). Increases in vascular growth and shading sometimes appeared to occur at the expense of mosses. However, mosses can also respond positively to warming and increased nutrient content when the availability of other resources, such as moisture and light, are favorable (Juutinen *et al.*, 2010).

Because of their limited time-frame, warming experiments represent ‘changed climate’ rather than ‘climate change’ (Frolking *et al.*, 2010) – that is, they measure physiological responses more than changes in vegetation as a result of altered competition and/or succession. Model simulations are necessary to explore such longer-term dynamics. Here we present a new simulation using the Biome-BGC model (Running & Hunt, 1993; Thornton, 1998) to examine the effects of warming on moss vs tree growth. Biome-BGC is a ‘big leaf’ model in which the canopy is modeled as two (sun and shaded) photosynthesizing surfaces. Growth, respiration, and mortality are fully integrated with the nitrogen cycle. Detritus flows to eight litter and soil pools, which vary in their turnover rates. The simulations reported here incorporate vegetation competition (Bond-Lamberty *et al.*, 2005; Table 1), allowing for changes in plant communities as well as disturbances. We simulated two different ecosystems: an upland black spruce forest with feather moss ground cover, and a forested peatland in which total NPP was roughly equally split between *Sphagnum* and black spruce (following data from Bond-Lamberty *et al.*, 2007). At the end of the spin-up phase, the upland had 18 kg C m<sup>-2</sup> in its soil, 0.20 kg C m<sup>-2</sup> of live moss, and 15.4 kg C m<sup>-2</sup> of live trees, while the simulated peatland had 26.3 kg C m<sup>-2</sup> in the top 1 m of peat, 0.62 kg C m<sup>-2</sup> of live moss, and 19.7 kg C m<sup>-2</sup> of live trees. NPP was dominated (c. 10×) by trees in the upland forest, although very cold and wet conditions favored mosses (Fig. 4a). The simulated peatland exhibited different competitive patterns. Precipitation increases alone had essentially no effect on NPP balance (Fig. 4b), while precipitation decreases initially resulted in trees benefiting at the expense of mosses. In Biome-BGC, most trees cannot grow in completely waterlogged soil. When drainage increases, soils become more oxic and trees are allowed to grow and transpire, which starts a positive feedback between tree



**Fig. 4.** Biome-BGC simulations of the effect of 100 yr changes in mean annual precipitation (MAP) and mean annual temperature (MAT) on competitive balance between mosses and trees for boreal well-drained forest (a) and poorly drained forested bog (b). The color scale is based on the logarithm of  $NPP_{\text{moss}}/NPP_{\text{tree}}$ , with light blue indicating moss-dominated net primary productivity (NPP) and dark blue indicating tree-dominated NPP. The white 'X' indicates current conditions for north-central Manitoba, surrounded by dashed ellipses showing interannual climate variation ( $1\sigma$ ,  $2\sigma$ ,  $3\sigma$ ). Gray areas indicate zero tree NPP. For the self-initialization (i.e. spin-up phase, c. 3000 yr), we used 1980–1999 meteorological data from the NCEP/NCAR Reanalysis Project (Kister *et al.*, 2001) with MAT ( $-3.7^{\circ}\text{C}$ ) and precipitation ( $490\text{ mm yr}^{-1}$ ) of north-central Manitoba, Canada. From this steady state, we ran 100 yr simulations in which the climate and soil drainage were varied for each run: MAT ranged from  $-5$  to  $+4^{\circ}\text{C}$  of normal, MAP from 40 to 200% of normal, and soil drainage rates spanned roughly an order of magnitude. These were run in a full-factorial design (c. 14 000 simulations total), with results ensembled (Thornton *et al.*, 2002) to account for interannual climate variability.

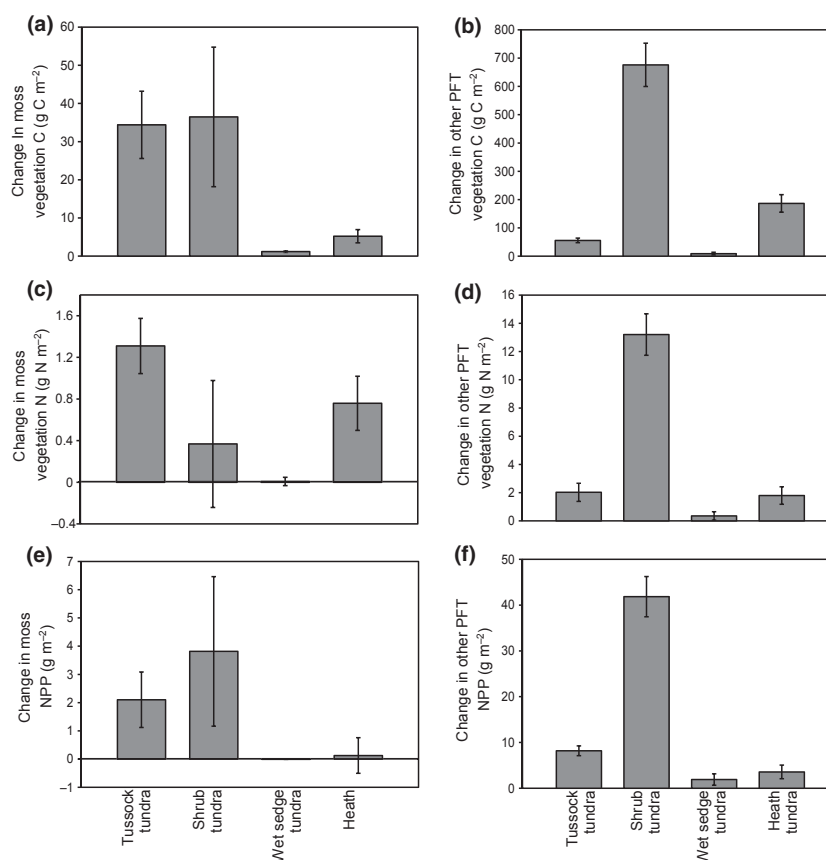
productivity and soil moisture conditions. As a result, a threshold effect exists in the model at c.  $400\text{ mm yr}^{-1}$ ; below this precipitation, the increasingly oxic soil supported greater tree growth and limited moss growth, resulting in strong increases in ecosystem ET (not shown). Below c.  $250\text{ mm yr}^{-1}$ , however, even trees started to be limited by the lowering water table. The temperature effect was simpler, with mosses always benefiting from colder temperatures (Fig. 4). In summary, the competitive balance between vascular and nonvascular plants was sensitive to changes

in air temperature and precipitation in the simulated forest and peatland. The ecosystem was resilient to change within the climate envelope observed for north-central Canada (ovals in Fig. 4), but tree NPP generally increased at the expense of moss NPP under moderately warmer and drier conditions.

Arctic climate is changing more quickly than at boreal latitudes (Serreze *et al.*, 2000). Increased shrub cover and productivity have been documented using remote sensing as well as plot-level observational studies and manipulations (Chapin *et al.*, 1995; Tape *et al.*, 2006; Hudson & Henry, 2009; Hill & Henry, 2010). These changes can cause reductions in moss abundance or growth through canopy shading and litter burial (Hobbie & Chapin, 1998; van der Wal *et al.*, 2005). To examine the effects of warming on competition between vascular plants and mosses in the Arctic, we build on the simulation reported by Euskirchen *et al.* (2009) to examine potential future changes in tundra moss and vascular productivity. The model domain spanned from the Arctic Ocean to the tundra-boreal forest ecotone in northern Alaska and was classified as 8% wet sedge tundra, 11% shrub tundra, 12% heath tundra, and 15% tussock tundra (with the remaining portion of the region including forest, barren ground, glaciers, and lakes). We used a version of the Terrestrial Ecosystem Model with a Dynamic Vegetation Component (TEM-DVM; Euskirchen *et al.*, 2009), which simulates multiple vegetation pools, soil thermal regimes, and PFTs that compete for nitrogen and light. Increases in shading as a result of increases in vascular productivity did not appear to be detrimental to moss growth in these simulated tundra environments (Fig. 5). The simulations showed that moss contributions to vegetation carbon, vegetation nitrogen, and NPP either increased (particularly in the tussock and shrub tundra types) or stayed the same across all ecosystems between the two time periods (Fig. 5). Changes in moss vegetation carbon, vegetation nitrogen, and NPP as a percentage of total vegetation change were generally small (1–3%; Table 2). In general, both the direction and magnitude of these simulations agreed with observational studies, showing increases in both moss and vascular biomass in the Arctic (Hudson & Henry, 2009). In the High Arctic in Norway, Prach *et al.* (2010) found no evidence of vegetation change, including moss, between the mid-1930s and 2008 attributable to climate change. Together, these results suggest that tundra mosses can be resistant to perturbation caused by warming and increases in vascular shading. It is possible that further increases in vascular biomass beyond those reported in Table 2 could begin to negatively impact moss productivity. Additional simulations that intentionally alter the growth or biomass of vascular PFTs could be valuable in identifying thresholds in vascular PFT biomass above which light limitations negatively impact mosses.

#### 4. The role of moss in northern regime shifts

Ecosystems tend to contain many feedback loops, although dominant feedbacks eventually emerge and cause systems to self-organize into a particular structure and function (Rietkerk *et al.*, 2004; see also Belyea & Baird, 2006). Perturbations that overwhelm or change these feedbacks may exceed the resilience of



**Fig. 5** Terrestrial Ecosystem Model with a Dynamic Vegetation Component (TEM-DVM) simulations of change in moss vegetation carbon (a), other plant functional type (PFT) vegetation carbon (b), moss vegetation nitrogen (c), other PFT vegetation nitrogen (d), moss NPP (e), and other PFT net primary productivity (NPP) (f) between 2003 and 2100 across tussock tundra, shrub tundra, wet sedge tundra, and heath tundra in northern Alaska. Following model calibration, we performed simulations based on a climate scenario that represents an 'intermediate' amount of warming (B2 Scenario; Nakicenovic & Swart, 2000) and the Hadley Centre for Climate Prediction and Research general circulation model version 3. Across the study region, from 2003 and 2100, air temperature increased by  $0.08^{\circ}\text{C yr}^{-1}$  averaged across seasons (greatest in autumn and winter,  $0.10^{\circ}\text{C yr}^{-1}$ ) and precipitation increased by  $1.3 \text{ mm yr}^{-1}$ . We performed model simulations for the years 1900–2100, and examined the data from the 'future' period, 2003–2100. (Error bars are  $\pm 1\text{SD}$ .)

**Table 2** Percentage of arctic moss and vascular plant contributions to total ecosystem vegetation carbon, vegetation nitrogen, and net primary productivity (NPP) in 2003–2013 (first decade of analysis) and 2091–2100 (final decade of analysis) by ecosystem type

Ecosystem type	Percentage of moss (vascular plant) contributions					
	Vegetation C		Vegetation N		NPP	
	2003	2100	2003	2100	2003	2100
Wet sedge	1.6 (97.6)	1.4 (97.5)	14.5 (85.7)	16.7 (83.8)	2.2 (97.5)	2.3 (97.5)
Tussock	33.1 (42.8)	34.0 (42.8)	35.2 (55.0)	35.1 (55.1)	23.4 (68.7)	21.7 (68.6)
Heath	2.7 (74.3)	2.5 (79.2)	11.7 (81.0)	15.0 (78.1)	9.7 (78.9)	8.5 (78.9)
Shrub	6.9 (90.6)	6.5 (91.7)	8.5 (81.9)	6.9 (83.8)	8.4 (83.7)	8.3 (86.7)

Other contributions not as a result of vascular plants or mosses are the result of lichens.

a system, causing it to be transformed to a new state with different properties and feedbacks (cf. Scheffer *et al.*, 2001). The term 'regime shifts' are often used to describe abrupt changes between contrasting, persistent states. Most disturbances do not cause lasting changes in ecosystem structure or function (Turner *et al.*, 1997). However, very severe disturbances or multiple disturbances that occur relatively quickly may cause regime shifts (Paine *et al.*, 1998; Frelich & Reich, 1999; Gunderson & Holling, 2002; Brown & Johnstone, 2011).

Northern high-latitude ecosystems have properties that convey resilience at varying spatial scales (e.g. long-lived, clonally reproducing plants; semi-serotinous cones of black spruce that disperse seeds post-fire). It seems likely that moss traits that influence nutrient immobilization, vascular recruitment and surface soil moisture also are important to the stabilizing feedbacks of northern forests, tundra, and wetlands. Because they produce biomass that, in general, decomposes slowly, mosses over time also contribute to the formation of microtopography,

**Table 3** Overview of regime shifts in northern ecosystems and the potential role of mosses in stabilizing one of the domains

Regime shift	Trigger	Likely stabilizing factors for the more moss-rich domain	Key references
Conifer → deciduous forest	Fire that consumes organic soil layer	High moisture content of some mosses inhibits deep combustion. Moss maintains low nutrients, peat accumulation, and poor-quality seedbeds	Johnstone <i>et al.</i> (2010)
Grassland → moss-dominated tundra	Climate and/or reduction of grazing	Mosses maintain cold, wet, and low-nutrient soils	van der Wal (2006)
Moss conifer forest → lichen woodland	Consecutive disturbances reduce black spruce seed pool	Mosses create conditions for slow decomposition and peat accumulation, and create poor quality seedbeds	Payette <i>et al.</i> (2000); Payette & Delwaide (2003)
Tundra → boreal forest	Vegetation–climate feedbacks	–	Bonan <i>et al.</i> (1992)
Tussock tundra → shrub tundra or forest	Climate, possible feedbacks with snow	Mosses maintain low nutrients, which may constrain shrub expansion	Sturm <i>et al.</i> (2001); Devi <i>et al.</i> (2008); Tape <i>et al.</i> (2012)
Permafrost lake/wetland → drained basin	Permafrost thaw and drainage	Mosses and thick peat layers help to stabilize permafrost	Jorgenson & Osterkamp (2005); Karlsson <i>et al.</i> (2011)
Permafrost forest/tundra → thermokarst lake or wetland	Permafrost thaw and flooding	Mosses and thick peat layers help to stabilize permafrost	Jorgenson & Osterkamp (2005); Karlsson <i>et al.</i> (2011)
Coastal marsh → exposed sediment	Grazing by snow geese	–	Jefferies, <i>et al.</i> (2006)

maintenance of seasonal ice and permafrost, and the formation of ombrotrophic conditions (see Section II). By contributing to these key ecosystem attributes, mosses play a role in both the resistance and the resilience of northern ecosystems.

We reviewed documented and hypothesized regime shifts for northern regions in the context of moss-related stabilizing factors (Table 3). In the majority of these regime shifts, mosses and their effects on soil temperature and nutrient cycling likely play a role in the dominant stabilizing feedbacks for one of the domains. The model simulations reported in this paper can also provide insights into how mosses contribute to ecosystem resilience and what changes to the moss community might mean for potential regime shifts. The models, for example, clearly indicate the importance of mosses in regulating moist cool soils (TEM results) or reducing water table variation (HPM results). In most cases, these moss impacts are indirect and are associated with accumulation of thick organic layers (i.e.  $\geq 20$  cm of surface peat). Under these conditions, Gornall *et al.* (2011) also suggested that mosses will have net negative effects on vascular plant communities. The model simulations also both showed that mosses were important to C and N accumulation. On the other hand, our simulations did not provide clear indications of regime shifts, even when the moss layer was completely removed. In the HPM simulation, loss of moss did cause the system to stop

accumulating peat, but only *c.* 500–600 yr after the onset of the disturbance. Even without moss, the simulated system functionally remained a peatland for several centuries. Similarly, in the TEM and Biome-BGC simulations, loss/reductions in moss also did not lead to abrupt changes in ecosystem function. A more sophisticated understanding of moss traits and relationships to ecosystem processes from both field and modeling studies will provide a platform that can be used to ask questions about the role of moss in dominant stabilizing feedbacks, how those feedbacks can be disrupted, and what that might mean for regime shifts.

#### IV. Future research needs

Different possible relationships between species diversity and resilience lead to several ecological hypotheses. The insurance hypothesis suggests that greater diversity ensures a greater range of responses to environmental perturbation, resulting in a positive relationship between diversity and resilience (cf. Yachi & Loreau, 1999; Hooper *et al.*, 2005). Alternatively, complementarity (niche differentiation, facilitation) among species in diverse communities might be disrupted with shifts in environmental conditions. In general, hypotheses about relationships between plant species diversity, resilience, and ecosystem



processes are based almost exclusively on vascular plants. Several recent studies have found positive correlations between moss species richness and ecosystem water retention by comparing monocultures to mixed assemblages of species (Rixen & Mulder, 2005; Michel *et al.*, 2012). Working with mosses to test hypotheses about diversity poses some logistical challenges, as moss species tend to be more difficult to manipulate and grow in experimental communities than most vascular plant species. However, moss transplant or species removal experiments may be valuable in examining the effects of diversity. Experiments that manipulate components of diversity, both evenness and richness (sensu Mulder *et al.*, 2004), would also be interesting in the context of understanding moss effects on community and ecosystem processes. Finally, there is a great need for understanding the role of moss in cross-scale resilience, particularly across trophic levels. Recent work has highlighted the role of moss in food webs (cf. Lindo & Gonzalez, 2010), but more work is needed before we have an understanding of the strength of interactions involving moss species, and how those interactions influence ecosystem stability (McCann, 2000).

Northern plant communities are often thought to have low functional redundancy. Functional redundancy refers to the notion that ecosystems will be more resilient if a function is fulfilled by multiple species (Walker, 1995; Naeem, 1998). If one species is eradicated, another species will be present in the community to provide the same function. For northern mosses, functional singularity (i.e. that species are individualistic in their effects on multiple functions) is likely to be equally important to evaluate. If moss communities have low functional redundancy or a high degree of functional singularity, how sensitive are those key species to environmental variation? Relationships between diversity and stability often have more to do with functional diversity than with a species diversity effect (cf. Tilman *et al.*, 1997; Wardle *et al.*, 1999). Thus, assessments of functional redundancy or singularity in moss communities require robust definitions of PFTs as a starting point. To achieve this, efforts to quantify traits across moss species are needed, particularly in light of a response–effect framework (cf. Suding *et al.*, 2008). As our understanding of response traits develops, can we use those traits to accurately predict changes in species abundance with environmental variation? Are the effects of mosses on ecosystem processes proportional to their local abundance or are there situations where species effects are disproportionate to their abundance (Suding *et al.*, 2008)? Greater insight into moss effect traits will influence how species are classified into PFTs (Cornelissen *et al.*, 2007), but could also affect how certain processes are represented in models. Finally, our understanding of all of these issues will benefit from a stronger understanding of phenotypic plasticity among traits. With environmental variation, some response traits might vary more within a species than among species. Assessment of trait plasticity will allow for informed decisions of how best to aggregate species, and whether using mean trait values is appropriate or not.

Throughout this paper, we have referred to a number of models that have included moss as a PFT (Table 1). As these and other models are used to address (or raise) questions of ecological

resilience, and the role of mosses in resilience, it is important to consider both parameter uncertainty for specific model processes (e.g. cuticular conductance of CO<sub>2</sub>, optimal water table for hollow *Sphagnum*) as well as conceptual uncertainty – that is, adequate representation of potentially important processes (e.g. moss spore dispersal, PFT establishment following disturbance and effects on nutrient cycling). Are the models more limited by uncertainty in the parameterization of the processes included or by what is not represented in the model at all? There are established methods for quantifying parameter uncertainty impacts on model results. These analyses are important to determine which parameters in a model are both influential (strong sensitivities) and poorly constrained by field and laboratory studies. On the other hand, of the many process not yet included in the few models discussed here, which are the most important to consider? ‘Hierarchical’ analyses (e.g. Wang *et al.*, 2009), in which a model is split into functional layers, may offer a way for moss and ecosystem modelers to evaluate the importance of, and uncertainty introduced by, the inclusion of particular processes.

Initial progress in representing mosses in DVMs and other models may come from tackling conceptual uncertainties. For example, the modeling simulations presented earlier in this paper suggest that loss of moss within northern plant communities will reduce soil carbon accumulation primarily by influencing decomposition rates and soil N availability. Despite being designed to examine processes at different timescales, two models (HPM and STM-TEM) both showed a significant effect of moss removal where it was an imposed condition. Results from the Biome-BGC and DVM-TEM suggest that northern, moss-rich ecosystems would need to experience extreme perturbation before mosses were eliminated. In field studies, moss community response to disturbance was varied (Fig. 3, Table S1), but moss was never/rarely eliminated from the system. Conceptual uncertainties related to these issues as well as other topics covered in the previous sections (e.g. controls on moss population viability, moss–vascular plant competition under changing resource availability, the role of microtopography in stability–resilience trade-offs) are important to consider in northern ecosystem models. As conceptual uncertainty is reduced, parameter uncertainty becomes more important to evaluate, which may require additional moss ecophysiology or other studies. For example, White *et al.* (2000) evaluated parameter uncertainty in Biome-BGC and found that vascular NPP is sensitive to leaf and fine root C : N, maximum stomatal conductance, specific leaf area, and percentage of leaf N in Rubisco. If similar conclusions were reached for moss parameterizations, do we understand enough about how these traits in mosses vary among species and environments to constrain model parameterization?

Using multiple models in analyses (model intercomparison projects) offers another approach for potentially reducing uncertainty (cf. Murphy *et al.*, 2004). Based on the results of simulations for a given region common to all models, are some models outliers while others show more agreement? At this time, it seems clear to us that moss models are not ready for intercomparison studies because they have been developed for different purposes.

Nonetheless, even without formal comparison, the results from the simulations reported here allowed us to explore moss responses to changing climate in tundra vs boreal regions (DVM-TEM vs Biome-BGC, respectively), while the comparisons between HPM and STM-TEM illustrated the role of mosses in carbon storage across longer vs shorter time-frames.

As noted throughout this paper, moss communities in many northern forests and peatlands are structured by environmental gradients defined by microtopography. In turn, microtopography stabilizes ecosystems in the face of perturbation during drought and wildfire. How can microtopography be parameterized in larger-scale models? Will cumulative stresses reduce the resilience of moss communities, microtopography, and thus northern ecosystems? What is the role of moss in potential tradeoffs between stability and resilience, and could interactions between climate change and disturbances make northern ecosystems vulnerable to new regime shifts? Related to all of these questions, what processes do models need to include to address compound disturbances occurring over decades, further compounded by a noisy trend in climate?

## V. Conclusions

Mosses in boreal and arctic ecosystems are ubiquitous components of plant communities, represent an important component of plant diversity, and have a strong influence on the cycling of water, nutrients, energy and carbon. While our simulations clearly indicated that loss of a moss layer in both boreal peatlands and forests would have profound influences on ecosystem processes and resilience, our literature review of moss community responses to disturbance showed all possible responses (increases, decreases, no change) within most disturbance categories in boreal and arctic regions. By combining literature review and synthesis with model simulations, this review has touched upon some key issues related to the role of moss in the stability and resilience of northern ecosystems. There are many more questions that deserve study in the realm of the 'bryosphere' (cf. Lindo & Gonzalez, 2010) and 'bryogeochimistry' (cf. Turetsky, 2003). Studies that employ a variety of approaches (such as paleoreconstructions, moss transplant and removal experiments, modeling studies and experiments) will be necessary to unravel the complex interactions among mosses, their environment, and ecosystem function. Mosses play a key role in long-term processes such as peat accumulation, the formation of microtopography and permafrost stability. It is therefore critical that future research approaches include models and experiments operating within a time-frame that is relevant to represent these processes and their associated feedback.

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## Supporting Information

Additional supporting information may be found in the online version of this article.

**Table S1** Synthesis of moss community responses following boreal and arctic disturbances

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