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Review

Sphagnum physiology in the context of changing climate: emergent influences of genomics, modelling and host–microbiome interactions on understanding ecosystem function

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ABSTRACT

Peatlands harbour more than one-third of terrestrial carbon leading to the argument that the bryophytes, as major components of peatland ecosystems, store more organic carbon in soils than any other collective plant taxa. Plants of the genus *Sphagnum* are important components of peatland ecosystems and are potentially vulnerable to changing climatic conditions. However, the response of *Sphagnum* to rising temperatures, elevated CO_2 and shifts in local hydrology have yet to be fully characterized. In this review, we examine *Sphagnum* biology and ecology and explore the role of this group of keystone species and its associated microbiome in carbon and nitrogen cycling using literature review and model simulations. Several issues are highlighted including the consequences of a variable environment on plant–microbiome interactions, uncertainty associated with CO_2 diffusion resistances and the relationship between fixed N and that partitioned to the photosynthetic apparatus. We note that the *Sphagnum fallax* genome is currently being sequenced and outline potential applications of population-level genomics and corresponding plant photosynthesis and microbial metabolic modelling techniques. We highlight *Sphagnum* as a model organism to explore ecosystem response to a changing climate and to define the role that *Sphagnum* can play at the intersection of physiology, genetics and functional genomics.

Key-words: bryophyte; climate change; genetics; nitrogen fixation; mosses; peatlands.

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INTRODUCTION

Almost one-third of all soil organic carbon is stored in northern peatland ecosystems – an estimated 455 to 547 Gt C in boreal bogs, fens and tundra wetlands (Gorham 1991; Yu 2012). Peatlands cover 400 million ha throughout the Northern Hemisphere and develop when net photosynthetic CO_2 fixation (net primary production or NPP) exceeds all forms of biomass loss (e.g. decomposition, erosion, wild fire) for thousands of years, resulting in the formation and accumulation of peat deposits that can be tens of metres thick (Rydin & Jeglum 2006; Limpens *et al*. 2008). This pool of stored organic carbon, much of it in a form that could be made readily available to microbial degradation, is vulnerable to globally rising temperatures, changes in local hydrology, increased occurrence and severity of wildfires and other disturbance regimes (McGuire *et al*. 2009). Current net flux of carbon to the atmosphere as CO_2 and CH_4 from northern peatlands is estimated to be 276 Tg C annually and could increase to 473 Tg C per year by the end of the century (Zhuang *et al*. 2006). Changes in the carbon balance of peatlands could provide a positive feedback to atmospheric forcing of climate if these ecosystems and their component organisms were to be destabilized by climatic change, land use or disturbance (Turetsky *et al*. 2012).

Sphagnum peat mosses are keystone species in peatland ecosystems and therefore exert a substantial impact on ecosystem function and net carbon (C) balance across the landscape (Clymo & Hayward 1982; Gorham 1991; Wieder 2006). Although several hundred species of *Sphagnum* exist, only a few dozen that are known to greatly influence ecosystem function have been studied within the context of physiology and environmental variation. It is well known that different *Sphagnum* species spatially organize along topographic gradients with water chemistry, pH, water table depth and surface moisture content as strong drivers of species distribution (Titus & Wagner 1984; van Breemen 1995; Hajkova & Hajek 2007). Field observations such as these have been

confirmed in greenhouse and growth chamber studies, where interspecific competition is evident in the response of *Sphagnum* to water table, precipitation and temperature (Robroek *et al*. 2007a,b). Because climate, hydrology, nitrogen deposition and disturbance can have dramatic consequences for plant community composition (Berendse *et al*. 2001) and the concomitant CO_2 and CH_4 fluxes (Strom *et al*. 2003; Koelbener *et al*. 2010), it is critical that the nature and, where possible, the genetic basis for *Sphagnum* growth, interspecific competition, plasticity and resilience be determined (Turetsky *et al*. 2012).

Multiple lines of evidence suggest that the distribution of *Sphagnum* species across environmental gradients is associated with physiological function. Poikilohydric plants (i.e. plants that cannot actively regulate their water uptake and loss), such as *Sphagnum* species, lack cuticle and stomata that regulate water loss (Titus *et al*. 1983); additionally, *Sphagnum* species lack roots for soil water extraction. Therefore, processes, such as photosynthesis, depend on the passive maintenance of tissue water content through the capillary uptake of water up from the water table, precipitation inputs and water storage by the plant. *Sphagnum* species have repeatedly been shown to achieve maximum photosynthetic rates across a broad range of tissue water contents (600 to 3400% dry mass) that decline rapidly with drought and desiccation (Titus *et al*. 1983; Murray *et al*. 1989; Schipperges & Rydin 1998; Maseyk *et al*. 1999). Recovery of physiological function following desiccation also appears to be an interspecific attribute, but has been studied in only limited detail (Schipperges & Rydin 1998; Robroek *et al*. 2009). Additionally, there are indications that *Sphagnum* photosynthesis is sensitive to low temperatures, but that high rates of photosynthesis may be maintained at temperatures up to 30 °C or higher (Harley *et al*. 1989; Hanson *et al*. 1999; Haraguchi & Yamada 2007). Recently, the influence of temperature has been extended to include effects on plant–microbe interactions, food web dynamics and nitrogen cycling within *Sphagnum* peatlands (Jassey *et al*. 2013). Admittedly, knowledge of individual and combined effects of increased temperature and changes in water relations on *Sphagnum* and its associated microbiome are major uncertainties in assessing the future role of peatlands in the global carbon cycle.

While *Sphagnum* serves a primary role in the carbon dynamics of high-latitude ecosystems (Bridgham *et al*. 2013), information on the physiological attributes of this bryophyte component of global peatlands is scarce. This has implications for our understanding of the *Sphagnum* species and their role in carbon cycle processes and in how the physiology and vegetative dynamics for this important plant functional type could be modelled (Williams & Flanagan 1998; Kuiper *et al*. 2014). In this review, we set the stage for developing a predictive understanding of the role *Sphagnum* plays in the vulnerability or resilience of peatlands to changing environmental conditions. We begin by reviewing our current understanding of *Sphagnum* population structure and genetic diversity. Our attention then turns to the physiological challenges of characterizing the photosynthetic behaviour of *Sphagnum* mosses that rely upon passive mechanisms to control the supply of water for maintaining function. The unique contribution of plant–microbe interactions to the carbon and nitrogen cycle in *Sphagnum* is described and a preliminary model is offered to potentially link these two frontiers. Finally, a strategy is presented where the sequencing of the *Sphagnum* genome could complement and expand genetic and physiological insights for bryophyte plant species.

SPHAGNUM POPULATION STRUCTURE AND GENETIC DIVERSITY

As in other mosses, the *Sphagnum* life cycle includes two stages that potentially result in dispersal and gene flow. Sperm is released into the environment by the paternal gametophyte and requires water to reach an egg. The zygote develops into an unbranched sporophyte that consists of little more than a sporangium, within which meiotic spores are produced. *Sphagnum* gametophytes can be either monecious, producing both egg and sperm, or dioecious. Gametophyte sexuality is generally a fixed species characteristic, although a few species, especially in the *Sphagnum* subgenus *Acutifolia*, appear to be hermaphroditic (Crum 1984). Of the 91 species of *Sphagnum* that occur in North America, 14 are known to have dioecious gametophytes, 58 have monecious gametophytes and the rest have unknown sexual conditions (McQueen & Andrus 1996). Species with dioecious gametophytes have high levels of intragametophytic selfing (which yields a completely homozygous sporophyte in one mating episode), although some outcrossing also occurs (Johnson *et al*. 2012). Monecious species have mixed mating systems with varying degrees of inbreeding. There are important interactions between microhabitat (elevated hummocks versus lower hollows) and mating patterns. An analysis of 14 species showed that inbreeding coefficients were higher in dioecious hummock populations than in dioecious hollow populations, but the opposite was true for monecious species: hummock populations had lower inbreeding coefficients than hollow populations (Johnson *et al*. 2012). Sporophytic inbreeding depression was demonstrated in the dioecious species, *Sphagnum lescurii* (Szövényi *et al*. 2009a).

Many *Sphagnum* species produce sporophytes (and spores) abundantly (Fig. 1). *Sphagnum* spores are variable in size but are generally about 25–40 μm in diameter and individual capsules (sporangia) hold some 50 000 to more than 200 000 spores (Sundberg 2005). Spore number is correlated with capsule diameter and empirical estimates suggest that spore dispersal distances are correlated with capsule size, possibly because of more effective explosive discharge as the capsule dehisce (Sundberg 2010). Spore size appears to be less of a determinant of dispersal distances, although more large spores are deposited at short distances (<3.2 m) from the source than smaller spores. At a site in central Sweden, the nine most abundant species produced 0.64 to 20 sporophytes per dm^2, with an estimated spore production at the site of some 16 million *Sphagnum* spores per m^2 (Sundberg 2002). Most spores fall close to the source but a significant number appear to travel great distances. Sundberg

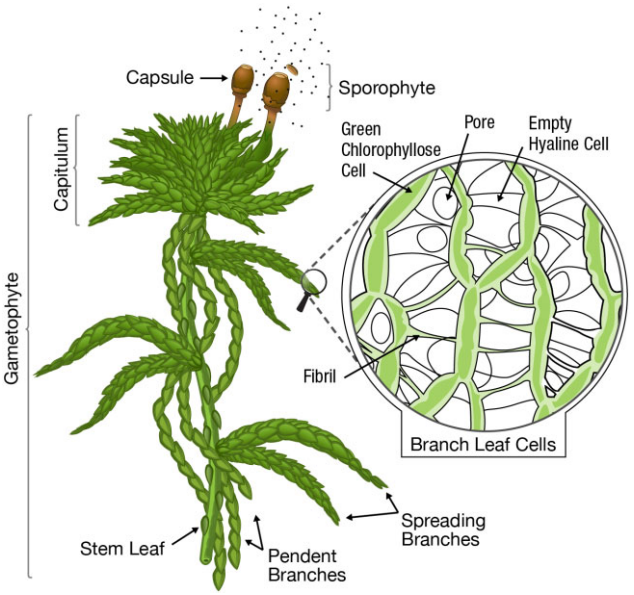

Figure 1. Schematic of *Sphagnum* plants. The *Sphagnum* plant consists of a stem, leaves, capitulum and sporophyte during reproduction. The inset shows the connected network of chlorophyllous photosynthetic cells and hyaline cells that are often filled with water to maintain plant water status. Hyaline cells that occur along the stem (not shown) contribute to ectohydric water transport.

(2013) estimated that about 1% of the *Sphagnum* spores that rain on the geographically isolated island of Svalbard originate from distant sources including intercontinental. *Sphagnum* spores remain viable for at least several years when buried, suggesting that a persistent spore bank exists under natural conditions (Sundberg & Rydin 2000). The fat-tailed dispersal shape (or kernel) characterizing *Sphagnum* spore distribution (as with other spore-producing plants) predicts that for isolated localities, colonists come from multiple, distant sources, generating a correlation between distance to the nearest spore source(s) and per colonist increases in genetic diversity. This 'inverse isolation hypothesis' (IIH) was supported in three of four *Sphagnum* species sampled from Sweden and from variously distant islands in the Baltic Sea (Szövényi *et al*. 2012).

The IIH also predicts that intraspecific genetic structure in *Sphagnum* will be strongly scale-dependent. At very local within-population scales, the genetic structure of colonies is determined by highly limited sperm movement, local spore dispersal and vegetative reproduction and immigration (Cronberg 1996; Ricca *et al*. 2008; Johnson *et al*. 2012). Within a single environment, almost all *Sphagnum* populations are multiclonal. For example, two groups of differentiated genotypes within *S. fuscum* occupy different positions along the height above water table gradient within a Swedish peatland (Gunnarsson *et al*. 2007). One hyperdiverse population of *S. macrophyllum* contains virtually all the microsatellite allelic variation present in the species throughout its range in the eastern United States (Johnson *et al*. 2012). Outbreeding depression demonstrated among matings within the population suggests that the population has served as a sink for colonists regionally (rather than a refugial source; Johnson *et al*. 2012). Clonal propagation clearly occurs and in some cases individual clones occur among geographically separated populations. At the extreme, all North American populations of *S. subnitens*, from Oregon northward through British Columbia and Alaska to the westernmost Aleutian Islands, appear to be a single clone (Karlin *et al*. 2011). European populations of the species are more diverse.

Within regions (e.g. Scandinavia, North American Pacific Northwest), most species show rather strong differentiation among populations (Stenoien *et al*. 2011; Terracciano *et al*. 2012; Shaw *et al*. 2014). Patterns of variation and the positions of replacement substitutions in the *GapC* gene in western European populations of *S. fimbriatum* suggest that non-neutral processes underlie its genetic structure (Szövényi *et al*. 2009b). Regional genetic structure within species with intercontinental ranges may differ between continents. *S. angermannicum* is extremely rare in Scandinavia and shows very strong differentiation among populations (mean Fst = 0.99), whereas *S. angermannicum* is more common in eastern North America and exhibits weaker differentiation among populations (Fst = 0.34). Significant isolation by distance within continental regions suggests dispersal limitation at the local and regional scales (Terracciano *et al*. 2012; Shaw *et al*. 2014). In the amphi-Pacific species, *S. miyabeanum*, the slopes of the regression of geographic on genetic distances differ between western North America and eastern Asia, suggesting differences in reproductive biology and/or patterns of local adaptation (Shaw *et al*. 2014). In that species, Alaskan populations are genetically more similar to Asian populations (Japan, China) than they are to North American populations from British Columbia and the western United States (Shaw *et al*. 2014). Significant, probably recent, migration was evidenced between Asian, Alaskan and western North American populations.

Phylogenetic inferences clearly show that intercontinental migration has occurred repeatedly in *Sphagnum* across geologic time (Shaw *et al*. 2008) and population genetic approaches document more recent migrations. Although statistically significant genetic divergence between conspecific *Sphagnum* populations in eastern North America and Europe occurs in a number of species, such differentiation is generally weak (Stenoien & Sastad 1999; Hanssen *et al*. 2000; Thingsgaard 2001; Szövényi *et al*. 2008; Stenoien *et al*. 2011). Intercontinental migration appears to be biased in the direction of Europe to North America in four unrelated species (Szövényi *et al*. 2008) but in the opposite direction for *S. angermannicum* (Stenoien *et al*. 2011). In *Sphagnum* species that occur on both sides of the Atlantic, eastern North American plants are typically more genetically variable than European plants.

Research on local adaptation in *Sphagnum* to date is virtually absent. Many or most *Sphagnum* species are clearly capable of effective dispersal over regional and even intercontinental scales and range shifts are likely to keep up with the changing climate in areas where suitable habitat remains. Nevertheless, species differ in mating systems, dispersal

ability, genetic variability and ecological tolerances and communities of co-occurring species are likely to change, with unpredictable outcomes in terms of ecosystem function.

THE PHYSIOLOGICAL ECOLOGY OF *SPHAGNUM*

A key question is how the aforementioned *Sphagnum* mating systems and genetic variability influence functional traits that determine in part, ecosystem function and their responses to variable environmental conditions. As the bryophyte traits that regulate biogeochemistry have been reviewed elsewhere (Cornelissen *et al*. 2007; Turetsky *et al*. 2008, 2012; Lindo *et al*. 2013), here, we focus on those physiological and morphological traits that drive carbon and nutrient metabolism. *Sphagnum* species generally occupy wet, acidic, nutrient-poor sites, where their dominance is attributed to efficient resource acquisition and retention, low turnover rates and low tissue palatability for herbivores (Coley *et al*. 1985; Grime *et al*. 1990; Fritz *et al*. 2014). *Sphagnum* expands into new territory through paludification, often associated with successional dynamics or areas affected by wildfire or altered hydrology (Crawford *et al*. 2003; Simard *et al*. 2007) or through terrestrial colonization from aquatic environments.

As the peatland develops, various microtopographical features emerge: especially lower, wetter, interconnected hollows and broad, expansive lawns or hummocks raised above the surrounding area (Fig. 2). Such features induce plasticity in functional traits and morphology within and across species that regulate their roles in ecosystem function (Cornelissen *et al*. 2007; Rice *et al*. 2008). For example, *Sphagnum* growing on hummocks often have greater stem, branch and leaf density and greater water retention capacity than those on the edges of hummocks or in hollows (Hayward & Clymo 1982; Luken 1985; McCarter & Price 2014). Differences in density and leaf nitrogen (N) content can lead to different rates of carbon uptake, nutrient acquisition and retention (Hajek & Beckett 2008). Interestingly, the differences in water retention traits can contribute to patterns of wildfire in bogs, such that desiccated hollows can be more susceptible to burning than hummocks (Benscoter & Wieder 2003).

Full occupancy of the land surface and strong capacity for uptake and storage of atmospheric N deposition may give *Sphagnum* a competitive advantage over co-occurring species (Fritz *et al*. 2014), although uptake capacities vary by species (Granath *et al*. 2009). Excessive N deposition is detrimental to photosynthesis and may reduce N fixation by associated bacteria (van der Heijden *et al*. 2000a). N deficiency strongly limits vascular plant growth in peatlands and N addition experiments have been shown to increase shrub and tree growth at the expense of *Sphagnum* (e.g. Berendse *et al*. 2001; Gerdol *et al*. 2008). Thus, the interception and storage of atmospheric N by *Sphagnum* may limit vascular plant expansion through competitive exclusion and slow loss of stored carbon. In addition to N, phosphorus (P) and/or potassium (K) is often co-limiting (Bragazza *et al*. 2004). P availability may enhance N assimilation in *Sphagnum* and slows the toxic impact of N deposition through time (Limpens *et al*. 2004).

Drying conditions and the loss of *Sphagnum* photosynthesis can provide a disproportionate control over net ecosystem exchange (NEE) when compared with co-occurring vascular plants (Kuiper *et al*. 2014). Reduction in water table depth results in shifts in species composition and loss of *Sphagnum* cover through time and may be exacerbated by warming temperatures (e.g. Weltzin *et al*. 2000). In alpine, boreal or polar habitats, *Sphagnum* often play a dominant role in early season NEE in the spring prior to vascular plant bud break and during periods when the roots of vascular plants are dormant (Moore *et al*. 2006). The lack of roots in this case uncouples *Sphagnum* from the underlying soil; however, this characteristic also indicates the critical link to surface water sources, a link that provides the primary controls on *Sphagnum* ecology, trait expression and C uptake.

Because *Sphagnum* species lack stomata, they have no direct control on evaporation and water flux from their leaves, although two key morphological features indirectly regulate water flow through the system. *Sphagnum* tissues contain specialized water-holding hyaline cells that serve to store water within the leaves, buffering evaporation and thereby maintaining the hydrated conditions required for photosynthesis. Water is supplied from the soil via capillarity along the exterior of the stems, branches and capitula (Proctor 1982), thus morphological traits related to individual and community density regulate capillarity of water to replace evaporative loss at the leaf surface (Thompson & Waddington 2008; Strack & Price 2009). Under drying conditions, traits related to pore diameter (Lewis 1988; Thompson & Waddington 2008), pore connectivity (McCarter & Price 2014) and cell wall rigidity (Hajek & Beckett 2008) provide limits on C uptake through cavitation or loss of cell turgor. Across species, there is wide variation in key morphological traits such as hyaline cell volume, capitulum density and plant height, with 10%, 50% or 500% variation across 10 species (Rice *et al*. 2008). The contribution of such morphological traits relative to the physiological induction of desiccation tolerance is a key question in these plants that lack stomata and prefer external ectohydric water redistribution. In a laboratory and field study using 13 species of *Sphagnum*, Hájek & Vicherová (2014) found that there is a morphophysiological trade-off by which hummock species rely upon desiccation avoidance via the aforementioned morphology, while hollow *Sphagnum* species rely more upon physiological-induced desiccation tolerance mechanisms.

In addition to tissue hydration, *Sphagnum* photosynthesis depends on CO_2 availability, leaf N content (especially the amount in rubisco or chlorophyll) and solar radiation. A key factor influencing *Sphagnum* CO_2 diffusion from the atmosphere to the rubisco catalytic sites is the rapidly dynamic water status of the plant. Typically, water conduction in *Sphagnum* is predominantly external through an interconnecting network of capillary spaces on the outside surface of the plants. This is in contrast to most vascular plants that have a relatively waterproof cuticle on epidermal cells forcing the

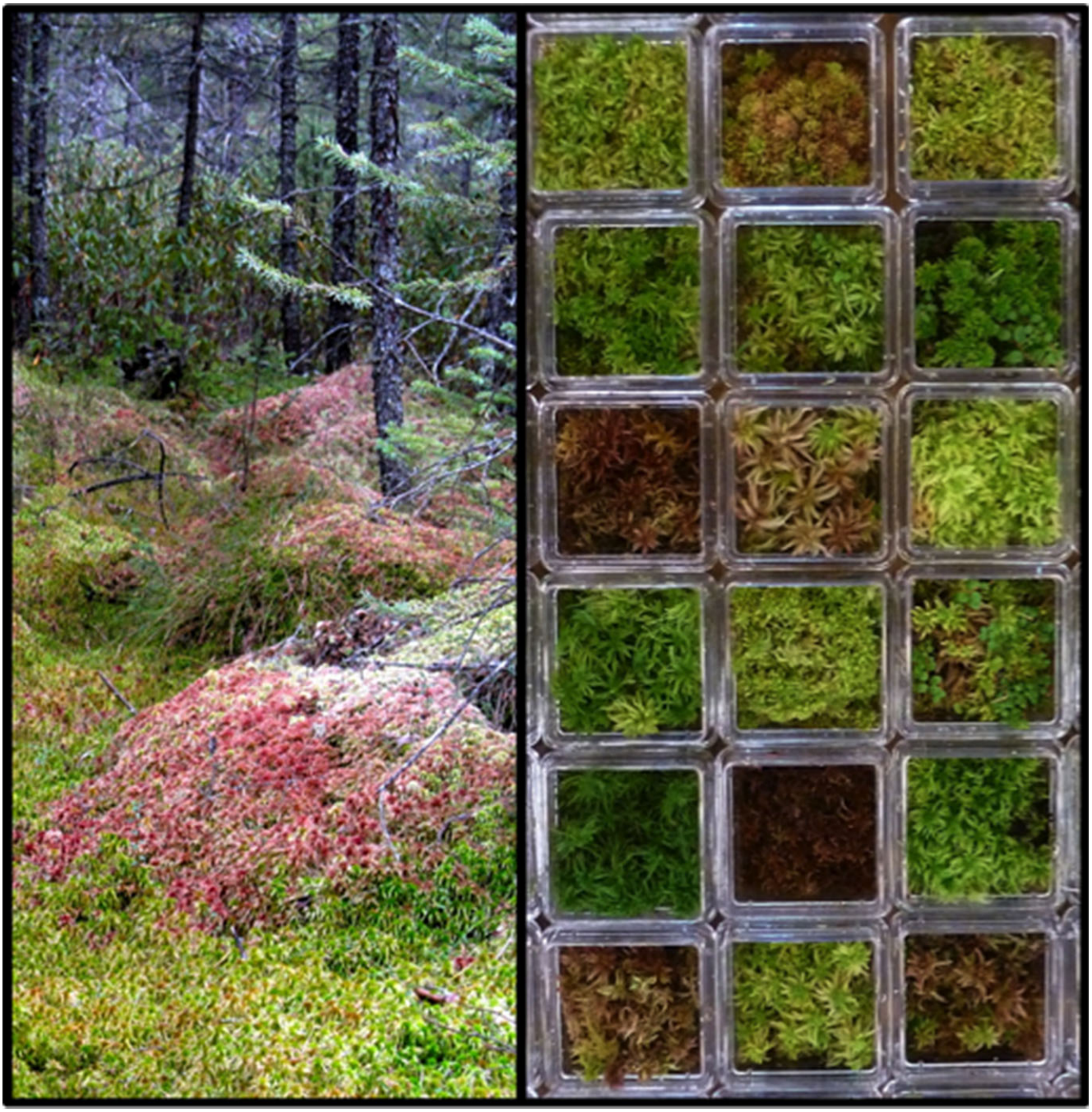

Figure 2. *Sphagnum* moss diversity at Marcell Experimental Station (MN, USA). Left: Example representation of hummock and hollow microtopographical features within an ombrotrophic bog. Right: Subset of species and phenotypic diversity present at this site.

majority of water conduction and gas exchange through the stomata. Because *Sphagnum* species lack cuticle and stomata, CO_2 diffusion from the atmosphere to the rubisco catalytic sites must pass an external water film that varies in thickness depending on environmental conditions (reviewed in Proctor 2009). Exposure of *S. recurvum* to elevated atmospheric CO_2 (700 μL L^{-1}) showed that an initial stimulation of photosynthesis was reduced to control levels after 3 d. This coincided with a shift in capitula N partitioning as observed by a reduction in total N and amino acids while soluble protein levels remained unaffected (van der Heijden *et al*. 2000b). Most photosynthetic activity occurs in the capitula (Hajek *et al*. 2009), although for some species the stem tissue below the capitula can also be important. In *S. balticum*, for example, 40% of C fixation occurred in the stems (Johansson & Linder 1980). *Sphagnum* can tolerate desiccation and high light, yet open-grown species tend to have lower chlorophyll, reduced efficiency of photosystem II (PSII) and lower photosynthetic capacity of those growing in more shaded conditions (Hajek *et al*. 2009). In general, bryophytes have lower

chlorophyll content and photosynthesis becomes light saturated at much lower photosynthetic flux densities (e.g. <650 μmol m^{-2} s^{-1}) than most vascular plants (Marschall & Proctor 2004), however, careful consideration of the expressed photosynthetic units must be accounted for (refer to Rice & Cornelissen 2014).

COMPLIMENTING MOSS HOST TRAITS WITH THE MICROBIOME

Plant health and productivity can be strongly affected by its associated microbial community, or microbiome, especially in the face of variable environmental conditions (Bulgarelli *et al*. 2013; Zelicourt *et al*. 2013). The interactions between the plant and microbiome can modify host plant physiological traits, including nutrient uptake (Carvalhais *et al*. 2013), growth allocation patterns and hormone metabolism (Spaepen *et al*. 2007), and enhance resistance to pathogens through competitive exclusion and 'priming' of the innate plant immune system (Berendsen *et al*. 2012). The plant microbiome contributes to many host plant phenotypes (Hardoim *et al*. 2008; Friesen *et al*. 2011; Weston *et al*. 2012) and can provide an important role in improved plant fitness in novel environments (Lau & Lennon 2012).

While the structure of dead peat overlaps with that of live *Sphagnum*, recent microbial community surveys of bogs show that rare operational taxonomic units (OTUs) varied between live surface material and dead peat suggesting different community function and specialization (Serkebaeva *et al*. 2013). Bragina *et al*. (2012) showed additional discrimination in the structure of microbial communities associated with different *Sphagnum* species, with *S. magellenicum* hosting an abundance of α- and Υ-proteobacteria while *S. fallax* was mainly colonized by Verrucomicrobia, Planctomycetes and Alphaproteobacteria. The same group of researchers found that there were no significant differences in microbial community composition in 16S rRNA or nitrogenase gene (nifH) amplification fragments from microbial communities colonizing *Sphagnum* species that occupy the same niche (*S. fallax* and *S. angustifolium*) (Bragina *et al*. 2012). As noted earlier, bogs often contain microtopographic (elevated hummocks and lower hollows) features that drive hydrological conditions. The functional consequences of how the hummock or hollow communities or tissue-specific communities [sporophyte versus gametophyte (Bragina *et al*. 2012)] impact ecosystem C and N cycles are not well understood. One common thread among the earlier studies of microbial community surveys is the abundance of acidophilic methanotrophic α-proteobacteria. These methanotrophs have been shown to convert CH_4-derived carbon into CO_2 that can be assimilated by the plant into photosynthate (Raghoebarsing *et al*. 2005; Kip *et al*. 2010).

Sphagnum species are known to persist in habitats with extremely low mineral nitrogen availability and its competitive success is partially dependent upon N acquisition through its association with nitrogen-fixing microbes (diazotrophs) (Lindo *et al*. 2013). *Sphagnum* is colonized by a variety of cyanobacteria on the cell surface and within water-filled hyaline cells (Granhall & Hofsten 1976) (Fig. 3). The non-living hyaline cells provide hydration to an interspersed network of living, photosynthesizing cells and are a necessary adaptation for water retention. Furthermore, these cells may provide a buffered environment compared with the extreme environment outside the plant that is characterized by fluctuating temperature spikes and high acidity (e.g. pH ~3.5 in ombrotrophic bogs). Cyanobacteria are known to fix atmospheric N_2 to NH_4^+ (ammonium) that can be used for its own N requirements or exchanged with its host for plant-derived carbohydrates (Meeks 1998). It has been shown that roughly 35% of the N fixed by cyanobacteria is transferred to its *Sphagnum* host (Berg *et al*. 2013). At the ecosystem level, this critical *Sphagnum*–diazotroph interaction can provide more N input to the bog than any other known N inputs (e.g. wet and dry N deposition or mineralization) (Hemond 1983).

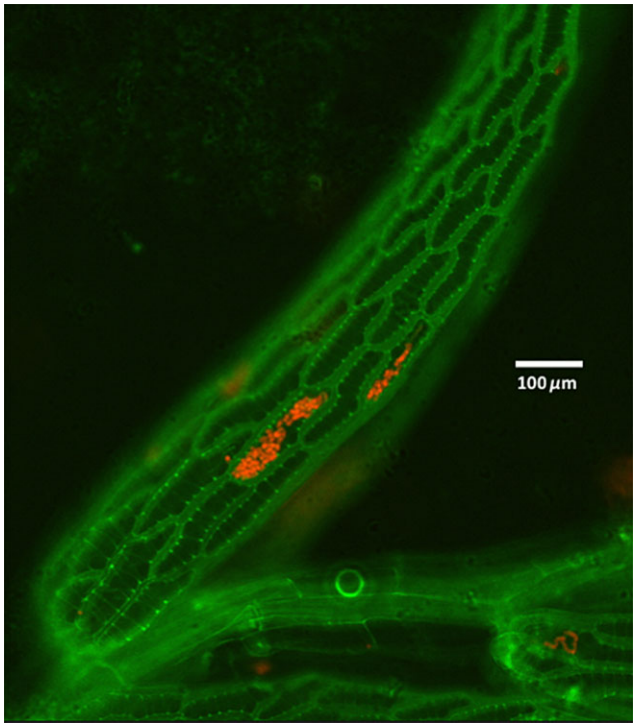

Figure 3. Composite micrograph of *Sphagnum fallax* leaf colonized with *Nostoc muscorum*. Chlorophyllous cells (green) with hyaline cells colonized by *N. muscorum* (red).

A current aspect of the *Sphagnum*–diazotroph interaction is how this critical association will respond to global climate change factors. As recently reviewed in Lindo *et al*. (2013), many bryophyte-cyanobacteria studies in high-latitude ecosystems find that maximal N_2 fixation rate per unit bryophyte mass is influenced by variable temperature, atmospheric CO_2, precipitation and atmospheric N deposition. Many of these associations are temporally dependent. Warming, for example, often shows increased N_2 fixation kinetic responses while longer term exposure results in reduced N_2 fixation rates and host bryophyte growth. Because only little is known about how variable environmental conditions and host species/genotype may regulate or modulate the exchange of

metabolites and signals between microbial associates and the host plant in general, we lack a predictive understanding of how future climate change scenarios could impact N acquisition and thus the cycling of C and N for these critical peatland ecosystems.

THE USE OF MODELS TO EXPLORE THE *SPHAGNUM*–MICROBIOME RELATIONSHIP

Sphagnum species and their associated microbiome provide a unique opportunity to scale mechanistic interactions from the plant-microbe scale to the ecosystem via peatland nutrient cycling. As an important example, the nitrogen budget in the well-characterized Thoreau's Bog (Hemond 1983) states that the majority of plant available N came from biological N_2 fixation, a striking illustration of the importance of plant–microbe interactions within a bog ecosystem. Nitrogen metabolism within the bryophyte host is tightly linked with carbon metabolism as amino acid biosynthesis requires not only inorganic N, but also C skeletons, reducing equivalents and ATP derived from photosynthesis or carbohydrate breakdown. By way of relative importance, N is in greater demand by most plants than any other mineral due, in part, to the large amount of N invested in the photosynthetic apparatus, especially in rubisco, which can account for up to 25% of leaf N (Sage *et al*. 1987). Plants need to balance the investment of N-containing proteins among different biological processes including photosynthesis, respiration, growth and defence (Chapin *et al*. 1990; Evans & Poorter 2001; Xu *et al*. 2012). These processes, in turn, influence developmental programmes and therefore population dynamics and long-term, ecosystem-level responses (e.g. NEE).

Photosynthesis models have been constructed for mosses and *Sphagnum* specifically, as high-latitude ecosystem studies suggest that moss layers contribute considerably to ecosystem CO_2 fluxes (Clymo & Hayward 1982). Such propositions led to the use of mathematical models to scale up individual measurements of photosynthesis and respiratory rates using largely empirical functions (Miller *et al*. 1984). The need to accurately represent environmental control on ecosystem gas exchange led to the development of mechanistic moss photosynthesis models (Tenhunen *et al*. 1994; Williams & Flanagan 1998). The Williams & Flanagan (1998) model uses the Farquhar *et al*. (1980) and Harley *et al*. (1992a) biochemical models within a *Sphagnum* carpet that includes (1) a light attenuation function to account for moss canopy structure and self-shading and (2) functions to account for the influence of tissue water content on CO_2 conductance and photosynthetic capacity. The water content functions are essential for accurate representation of poikilohydric mosses that do not have the stomata or vasculature to actively control tissue water status and CO_2 diffusion to rubisco catalytic sites.

As motivated by this review, we have begun to explore how coupling mechanistic models of plant photosynthesis with a bacterial metabolic model of a representative N_2-fixing microbial associate (diazotroph) influences metabolism and plant productivity. We use these simulations to formalize our current understanding of the plant and diazotroph association on host plant growth and productivity and highlight areas that need further experimentation and understanding. The availability of microbial genome sequences has enabled the construction of bacterial-specific flux balance analysis models. These models, when parameterized with sufficient data, can be used to predict metabolite fluxes through given metabolic pathways, primarily those in core metabolism. Detailed descriptions of the use and construction of genome-based metabolic models has been extensively reviewed (Oberhardt *et al*. 2009; Henry *et al*. 2010; Thiele & Palsson 2010; Hamilton *et al*. 2013) and rapid construction of these models is available to the scientific community through the open source KBase cyberinfrastructure project (www.KBase.us). Cyanobacteria of the genus *Nostoc* can associate with *Sphagnum* (Granhall & Hofsten 1976; Lindo *et al*. 2013) and provide nitrogen to the plant through fixation of atmospheric N_2. We use the published *Sphagnum* photosynthesis models in conjunction with predicted rates of microbial N fixation to investigate the important *Sphagnum*–diazotroph relationship.

Insight 1: The consequence of N-fixing microbial abundance on *Sphagnum* productivity

Numerous studies suggest that climate change drivers may disrupt the *Sphagnum*–diazotroph association and have been extensively reviewed (Lindo *et al*. 2013; Rousk *et al*. 2013). Indeed, the relationship between N and photosynthetic capacity is a key driver of uncertainty in C cycle modelling (Zaehle *et al*. 2005; Rogers 2014). Modifying the plant and diazotroph association in the field is difficult but we can explore the consequence of this disruption by estimating the effects of decreasing diazotroph cell numbers associated with *Sphagnum*.

Using the Williams & Flanagan (1998) *Sphagnum* photosynthesis model with added N parameterization as detailed in the Appendix, we simulated high daily rates of net primary productivity (NPP) in response to variable light attenuation conditions, tissue nutrient status (i.e. C : N) and N partitioning. *Sphagnum* C : N ratios and partitioning of leaf N to rubisco were major drivers of variability in our model of C uptake as NPP (Fig. 4a,c). Further drivers of variability in the model were the stem area index (SAI) and the *Sphagnum* 'stand' light extinction coefficient (k), both of which scale stem-level C assimilation to the 'stand' or ecosystem level. Increasing k decreased NPP while increasing SAI increased the variation caused by varying k (Fig. 4a). The k determined by Williams & Flanagan (1998), 1.5, is substantially higher than commonly used for tree canopies (e.g. 0.5) and needs further characterization in *Sphagnum* stands or carpets for accurate modelling. The SAI is also important for scaling and is complicated by the difficulty in measuring *Sphagnum* stem area and determining the depth of live, actively photosynthesizing biomass in the field.

A genome-based model has been developed for a non-plant-associated diazotrophic cyanobacteria and predicts nitrogen fixation rates of 1.43 mmol N_2 (g DW per bacteria)$^{-1}$ h^{-1}

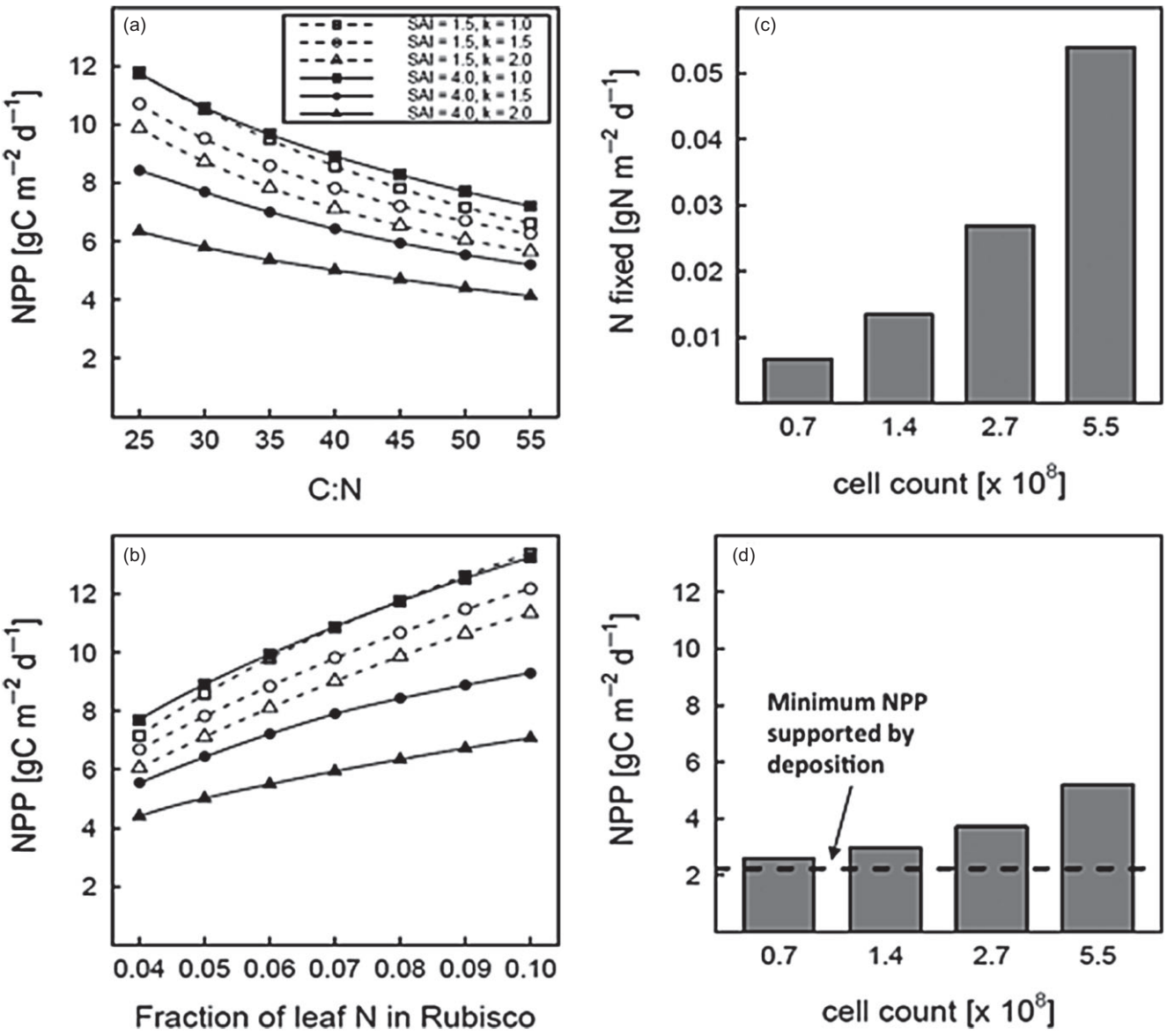

Figure 4. Simulated net primary production (NPP) variation in response to *Sphagnum* C : N ratios and stem area index (SAI) (a) and the fraction of leaf N in rubisco (b). The influence of varying SAI from 1.5 (dashed lines and open symbols) to 4 (solid lines and closed symbols) is shown combined with the influence of the light extinction coefficient (k; 1, squares; 1.5, circles; and 2, triangles). (c) Biological fixation of nitrogen as a function of cell number (d) potential impact of *Nostoc* dissociation on *Sphagnum* productivity. Complete plant model description is provided in the Appendix.

(Vu *et al*. 2012), the value that we will use as a proxy for *Nostoc* N fixation rate in these calculations. This rate is similar to the observed rate for two plant-associated diazotrophs (0.17–0.24 mmol N_2 (g DW per bacteria)$^{-1}$ h^{-1}; Resendis-Antonio *et al*. 2007; Zhao *et al*. 2012). Given a predicted *Sphagnum* CO_2 fixation rate of 6.03 g C m^{-2} d^{-1} (NPP estimated at a fixed C : N ratio of 55; Kuhry & Vitt 1996), a light extinction coefficient (k) of 1.5, an SAI of 4 and a deposition/biological fixation (57%/43%) rate consistent with the N budget observed in bog systems (Hemond 1983; Stewart *et al*. 2014), we estimate that ~0.06 g m^{-2} d^{-1} of N is required to meet the observed growth demand for *Sphagnum*. Using the N fixation rate for a diazotrophic cyanobacterium described earlier (Vu *et al*. 2012), the plant would need to harbour ~2.7×10^8 microbial cells per gram DW of plant material. While we do not have yet the estimates of microbial biomass in the natural *Sphagnum* system, this estimate is similar to the published results for important bacterial associates in the endosphere of vascular plants (Kristin & Miranda 2013). Furthermore, this estimate only accounts for photosynthetically active tissues and the nitrogen-fixing bacteria may be associated with lower peat levels and still contribute nitrogen to the plant through ectohydric water transport. New research directions should focus on identifying the location and distribution of bacterial associates of *Sphagnum*.

As described by Lindo *et al*. (2013), multiple factors could affect the association of *Sphagnum* and their nitrogen-fixing associate. We explored this scenario by asking how decreasing microbial abundance could decrease CO_2 fixation in peatland systems. As shown in Fig. 4b, decreasing cell numbers is predicted to decrease total N_2 fixation until photosynthesis is supported only by deposition (Fig. 4d). In this analysis, we assumed that total *Sphagnum* biomass was constant, and thus a change in N fixation rate would proportionally decrease NPP. While the quantitative effects of climate change on the *Sphagnum*–diazotroph association are yet unknown, it is clear that decreases in microbial cell abundance could have a substantial impact on ecosystem productivity.

Insight 2: Challenges in modelling C and N interactions through the *Sphagnum*–diazotroph interactions

It is important to note that the nitrogen fixation rates for *Nostoc* or other *Sphagnum*-associated nitrogen fixers on plants are variable and are dependent upon environmental and genetic interactions. The earlier simulation provides a formalization of our current understanding and models parameterized to experimental data for this system must be produced to add confidence and uncertainty estimates in such calculations. Nonetheless, this preliminary calculation highlights the importance of this association and how climate change drivers may mechanistically affect *Sphagnum* productivity. Field measurements of microbial biomass will complement these estimates, further allowing us to understand the plant–microbe interactions and their importance to the system. Disagreements in models and measures may suggest interesting mechanisms for this relationship which will help us understand the costs and benefits for this complex multi-organism interaction that are so important to peatland C and N cycling.

An interesting complication of coupling stem-level models and microbial flux models is the vast difference in scale, both spatially and temporally. The stem models presented here consider mechanistic drivers of photosynthesis (CO_2 diffusion, water content, etc.) to predict carbon fluxes at the canopy level (cm to m). The microbes associated with *Sphagnum* interact with their host at the micron level, within individual hyaline cells or on cell surfaces and under conditions that vary widely over short distances. The second major scale separation is time scale: cyanobacteria *Nostoc* have doubling times on the order of hours (Summers *et al*. 1995; Yu *et al*. 2009), while *Sphagnum* grows much more slowly. This has important implications when we consider the rate of bacterial turnover within the system, nutrient cycling and transport, and spatial distribution of bacterial biomass throughout the ecosystem. We also note that other nutrients will be important in the exchange between the plant and microbiome as well as translocation of nutrients from senescing plant material.

A major challenge in developing stem-level photosynthesis models is how to infer key model parameters from measurable variables such as chlorophyll fluorescence, isotope discrimination and gas exchanges. During such measurements, the water film of the tissue will tend to shrink as it retreats inwards with time because of evaporation. This retreat can result in dynamic surface resistance to gas exchange over the course of a day or during a drying cycle (discussed earlier). Therefore, parameter estimation will need to explicitly consider an increasing or decreasing water thickness in order to reliably estimate photosynthetic parameters.

It may be particularly important to consider the effects of spatial separation between rubisco and the releasing site of CO_2 from dark respiration and photorespiration, and on the estimation of total tissue conductance to CO_2. This separation means that at least in theory, the tissue conductance is a composite variable, rather than a primary parameter (Tholen *et al*. 2012). In vascular plants, mitochondria often occupy the centre of the cell while chloroplasts are positioned just under the plasmalemma (Nobel 2009), effectively surrounding the mitochondria. In this configuration, CO_2 molecules evolved from mitochondria and released into cytosol have to pass through chloroplasts to escape from the cell. From a modelling point of view, this arrangement has the same effect as if rubisco and mitochondria shared the same compartment and a single mesophyll conductance parameter is suggested to be sufficient to model CO_2 diffusion inside vascular plant leaves (Cernusak *et al*. 2013; Gu & Sun 2014; Sun *et al*. 2014). However, it is not known whether *Sphagnum* chloroplasts are arranged directly against the plasmalemma within chlorophyllous cells. Furthermore, there is uncertainty in the CO_2 diffusion resistance associated through chlorophyllous and hyaline cells. Thus, it may be necessary to use multiple parameters to describe CO_2 movement inside bryophyte tissues, for example, with one component representing the path from the cytosol through the chloroplast envelope and then stroma to rubisco inside the chloroplast and another representing the path from the water film through the cell wall and plasmalemma to the cytosol. New approaches will need to be developed to estimate these components of the total tissue conductance.

The promise of genomic ecology for peatland ecosystems

It has been suggested that an organism's potential to adapt is defined by its core genome (nuclear, chloroplast, mitochondria) plus the genomes of symbionts that form intimate associations and provide complementary functions that the host cannot perform (Martin *et al*. 2004; Cheng & Tuskan 2009). Therefore, a holistic characterization of the core genome as well as endophytic associates is necessary in order to define an organism's adaptive potential. Recent advances in genome and microbiome sequencing provide exciting opportunities in ecological genomics. These advances have been widely adapted in efforts to improve food, fibre and fuel production to meet the needs of an expanding population where DNA marker systems have been routinely used to identify superior genotypes for use in crop improvement in

the face of climate change (Henry 2014). Unlike their counterparts targeted for food, fibre and fuel production, species such as *Sphagnum* that play a fundamental role in the global carbon cycle often lack rich genetics and genomics resources. The disparity is particularly unsatisfactory given that nearly all plant-related processes implicated in carbon assimilation and microbial-mediated nutrient dynamics listed earlier have a demonstrated genetic basis (Franks *et al*. 2014).

Therefore, the inception of the *Sphagnum fallax* genome sequencing project, supported by the Department of Energy (DOE) Joint Genome Institute, represents a crucial and timely first step in addressing contemporary challenges resulting from climatic change. Genome-enabled ecological studies in *Sphagnum*, via leveraging rapidly evolving genome sequencing techniques and robust computational analyses to (1) characterize genetically driven variation in natural populations of undomesticated organisms and (2) predict genotype-to-phenotype relationships, will lead to a trait-based understanding of the role of non-vascular plants in ecosystem function.

Signatures of selection

In their favour, undomesticated plants such as *Sphagnum* present an unparalleled opportunity to evaluate the effect of macro- and microenvironmental factors on climate-driven natural selection without the artefacts created during domestication (e.g. genetic bottlenecks). Using a high resolution references, coupled with sampling via resequencing genotypes from varying habitats, signatures of local selection on a given population can be identified. Focusing on such genetic loci can lead to direct characterization of specific genes or plant functional traits under a particular environmental attribute (Yoder *et al*. 2014). Expanding these samplings across multiple locations and populations will ultimately lead to the identification of genomic regions exhibiting patterns of active selection across naturally occurring environmental clines. Signatures of selection can also be characterized over time, by establishing baseline genetic variably of the species at one time point and then resampling the same population after a fixed period of time to estimate changes in allele frequencies and associated phenotypes. By taking a similar approach, Nevo *et al*. (2012) observed significant shifts in flowering time within in a population of wild cereals sampled over a 28 year period. Reciprocal transplanting of resequenced clones in 'space for time' studies (Franks *et al*. 2014) can also be used to simulate genome evolution in response to climate change. This information can be useful in predicting shifts in population structure under given climate scenario and aid in the development predictive models to guide implementation of appropriate management strategies.

Deconstructing compound genetic effect for vegetation models

With exceptions, the majority of traits involved in carbon cycling are quantitative (meaning they are mediated by numerous genes) and display normal distributions over a range of phenotypic values from lowest to highest (Harrisson *et al*. 2014). Traits such as chlorophyll content, nitrogen-use efficiency, drought and freezing tolerance are classic quantitative traits that fall under the control of many genes whose expression can be modulated by the environment. This property of heritable and environmental determination presents challenges in climate models. Vegetation models, for example, typically prescribe plant functional types (PFTs) that are used to classify plants into broad categories of species with similar physiological and phenological characteristics. Such groupings are often defined by the averaging of numerous attributes (e.g. organ C to N ratio, photosynthetic characteristics) across many species and ecotypes. However, field experiments and pollen records indicate that species and genotypes within species often respond individually to changes in environment (Bret-Harte *et al*. 2008) and such averaging is known to contribute to considerable uncertainty in land model predictions of ecosystem function (Zaehle *et al*. 2005; Kattge *et al*. 2009). Because such models use an aggregated single coefficient, they are insensitive to shifts in population-level allele frequencies that may culminate in subtle shifts in the parameter mean or broader values at the extremes.

The raw material for diversity can be deconstructed into single nucleotide polymorphisms (SNPs) that represent difference among genotypes or species at a particular position of the genome. Such variants (i.e. mutations) accumulate over time from the ancestral genome and can be beneficial, neutral or detrimental depending on the effect of gene function and the environment in which the genotype occurs. These mutations can be readily defined using whole-genome resequencing techniques and are defined as allelic variants among alternate genotypes. Depending on an organism's environment, certain mutations will be selected for or against leading to a detectable deviation from expected frequencies within the population. Szövényi *et al*. (2009b) described such changes for the GapC gene described earlier. Advances in quantitative genetics-based phenotype-to-genotype modelling have been developed that account for allele differences by assigning a 'value' to each allelic variant based on individual contribution to overall phenotype (i.e. percent phenotypic variance explained). Such modelling techniques have the potential to transform single-value PFT representation into genomically informed trait-based representations.

Among the biggest threat of climate change is the prospect of keystone species extinction leading to disrupted ecological stability (Whitham *et al*. 2006). It has long been recognized that the risk of extinction is directly related to diversity in the gene pool. An empirical evaluation of genetic diversity across species' ranges is the necessary first step in identifying vulnerable populations and prioritizing germplasm for safeguarding. For example, it can be surmised that the shallow gene pool characterizing the apparently clonal population of *S. subnitens* in the Pacific Northwest described earlier (Karlin *et al*. 2011) represents a vulnerable ecological zone that is unlikely to cope with extreme environmental changes. However, low resolution characterization based on

microsatellite markers is unlikely to reveal the hidden population structure that underlies most natural populations. In this case, deep resequencing of representative genotypes across the range to evaluate the true extent of this clonality would establish the presence or absence of cryptic variation that could affect predicted outcomes based on low resolution characterization. Furthermore, the key processes of gender determination, whose genetic basis is well established, may determine patterns of habitat colonization and species expansion discussed earlier. This has wide implications for *Sphagnum* species because molecular markers predictive of gender can be readily incorporated into vegetation models to estimate potential for species spread, vulnerability to inbreeding resulting in near clonal populations and potential for recombination leading to novel adaptive traits.

CONCLUSIONS

The importance of *Sphagnum* and *Sphagnum*–microbial interactions to peatland function, carbon and nitrogen cycling, and therefore climate have recently been highlighted (Turetsky 2003; Limpens *et al*. 2008; Turetsky *et al*. 2012; Lindo *et al*. 2013). What we lack is a formal modelling representation of this knowledge that includes the mechanistic insight of the physiological processes that ultimately drive community interaction and ecosystem function under variable climatic conditions. In this review, we point to the areas where we need more understanding such as a better representation of CO_2 diffusion pathways and how they are influenced by the environment and stand/canopy structure, the magnitude of inter- and intraspecific genetic variation and how that variation translates to physiology, expression of functional traits and adaptive evolution. We also highlight the importance of the microbiome, especially in bog and peatland systems that rely heavily on biological N_2 fixation. We still do not fully understand the genetic and environmental drivers mediating critical plant–microbiome interaction. Genomics and population genomics have the potential to provide trait-based characteristics that may improve vegetation models. Here, the opportunity lies in leveraging advances from agronomic and bioenergy feedstocks that have a wealth of genomic and phenotypic data for application to an ecosystem-relevant species, in this case *Sphagnum*.

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APPENDIX

Modelling Appendix

Sphagnum *photosynthesis model description*

The model is based on the enzyme kinetic models of photosynthesis (Farquhar *et al*. 1980), scaled using Beer's law scaling of light extinction through a canopy subdivided into layers according to the stem area index (SAI) of the *Sphagnum* 'canopy' (Williams & Flanagan 1998). Net CO_2 assimilation (A, μmol CO_2 m^{-2} s^{-1}) is the minimum of the rubisco limited gross carboxylation rate (W_c, μmol CO_2 m^{-2} s^{-1}) and the electron transport limited gross carboxylation rate (W_j, μmol CO_2 m^{-2} s^{-1}), scaled to account for photorespiration, minus mitochondrial (dark) respiration (R_d). Parameter values are available in Table A1. The net assimilation function takes the form:

$$A = \min\{W_c, W_j\}\left(1 - \frac{\Gamma_*}{C_c}\right) - R_d \quad (1)$$

where Γ_* is the CO_2 compensation point (Pa) in the absence of mitochondrial respiration, the C_c at which the carboxylation rate is balanced by CO_2 release from oxygenation. Both W_c and W_j are modelled as functions of the chloroplastic CO_2 partial pressure (C_c – Pa). W_c follows a Michaelis–Menten function of C_c in which $V_{c\max}$ (μmol CO_2 m^{-2} s^{-1}) determines the asymptote:

$$W_c = V_{c\max}\frac{C_c}{C_c + K_c\left(1 + \frac{O_i}{K_o}\right)} \quad (2)$$

where O_i is the intercellular O_2 partial pressure (kPa); K_c and K_o are the Michaelis–Menten constants of rubisco for CO_2 (Pa) and for O_2 (kPa). K_c and K_o were calculated after Bernacchi *et al*. (2001) and Γ_* after Brooks & Farquhar (1985). The light-limited gross carboxylation rate (W_j) is a function of the electron transport rate (J, μmol e m^{-2} s^{-1}) following a similar function of C_c where the asymptote is proportional to J:

$$W_j = \frac{J}{4} \times \frac{C_c}{C_c + 2\Gamma_*} \quad (3)$$

J is a function of incident photosynthetically active radiation (I – μmol photons m^{-2} s^{-1}) that saturates at the maximum rate of electron transport ($J_{\max}$, μmol e m^{-2} s^{-1}), formulated by

Harley *et al*. (1992b) following Smith (1937), although other formulations exist:

$$J = \frac{\alpha I}{\left(1 + \frac{\alpha^2 I^2}{J_{\max}{}^2}\right)^{\frac{1}{2}}} \quad (4)$$

where α is the apparent quantum yield of electron transport [assumed to be 0.24 mol electrons mol^{-1} photons by Harley *et al*. (1992b) although α is not invariant in nature and should be better characterized for *Sphagnum*] and is the result of multiplying the true quantum yield and light absorption by the leaf. The exponents in Eqn 4 are empirical values and represent the transition from light-limiting to CO_2-limiting conditions. Equation 4 is used to predict leaf-level photosynthesis.

V_{cmax} was calculated in the method of Community Land Model (CLM) (Oleson *et al*. 2010):

$$V_{c\max} = N_a f_{lnr} f_{nr} a_r \quad (5)$$

where N_a is the leaf nitrogen (g N m^{-2}), f_{lnr} is the fraction of leaf N in rubisco, f_{nr} is the molecular weight ratio of rubisco to the N in rubisco and a_r is the specific activity of rubisco. The equation assumes that all rubisco is active so the specificity implicitly includes activation. The specific activity used within is 60 μmol CO_2 g^{-1} rubisco s^{-1}, which assumes a k_{cat} of 4. 1 s^{-1} at 25 °C (Oleson *et al*. 2010). This k_{cat} value is 87.5% higher than that used by Farquhar *et al*. (1980) and 43.7% higher than the value for bryophytes measured by Galmés *et al*. (2014). We chose a value of k_{cat} so that our model was somewhat comparable with CLM4.0 and 4.5, although the true value of k_{cat} for *Sphagnum* clearly represents another source of uncertainty in the *Sphagnum* productivity model. Temperature sensitivity for V_{cmax} was based on Medlyn *et al*. (2002) and equations and parameters for Scots pine which occupy similar climatic environments.

R_d was assumed to be 10% of V_{cmax} (Williams & Flanagan 1998).

C_c is determined by the gas diffusion law:

$$C_c = C_a - \frac{A}{g_i} \quad (6)$$

where C_a is the atmospheric CO_2 partial pressure (Pa) and g_i is the internal conductance to CO_2 (μmol CO_2 m^{-2} s^{-1}). We used the empirical function of fresh weight to dry weight ratio (W) of Williams & Flanagan (1998), assuming a ratio of 5, to calculate g_i:

$$g_i = 10^3(-0.195 + 0.134W - 0.0256W^2 + 0.00228W^3 - 0.0000984W^4 + 0.00000168W^5) \quad (7)$$

g_i is highly affected by water content, hence the need for a complex polynomial to describe the relationship.

Scaling of instantaneous leaf-level rates

We follow Williams & Flanagan (1998) and use Beer's law scaling of photosynthetically active radiation (PAR) through the canopy, dividing the canopy into layers by SAI:

$$I_l = I_0 e^{-k(l-1)} \quad (8)$$

where I_l is the incident PAR in canopy layer l, I_0 is the PAR at the top of the canopy and k is the extinction coefficient (1.5 after Williams & Flanagan 1998). This formulation assumes direct beam radiation only, that the top canopy layer receives incident PAR and that there is no self-shading in the top layer. The spatial resolution using this method is ~10 cm per SAI. Nitrogen was not assumed to vary with canopy layer as there was little evidence to support this from the Spruce bog (Norby, unpublished results). Leaf N_a in Eqn 5 was calculated in each canopy layer as $1/(C:N\ SLA)$ where the $C:N$ is the *Sphagnum* C : N ratio and SLA is the specific leaf area (m^2 g^{-1} C) calculated as the standing live biomass, divided by the SAI. Standing live biomass was estimated to be 175 g C m^{-2} (Norby, unpublished results) and the SAI as 1.5 (Williams & Flanagan 1998).

I_0 is calculated from the solar constant adjusted for latitude (50 °N) and time of year (Julian day 150). To scale instantaneous rates of photosynthesis to daily rates, assimilation (Eqn 1) was calculated at 25 time points during the day, scaling I_0 according to the solar elevation angle and then integrating the time course of instantaneous rates to obtain a daily integral. Night time respiration was assumed to be at the same rate as during the day. A mean daily leaf temperature was assumed at 15 °C.

Table A1. Parameter values

Parameter	Value	Units
α	0.24	mol e mol photon^{-1}
a_r	60	μmol CO_2 m^{-2} s^{-1} g^{-1}
f_{nr}	0.04–0.10	unitless
f_{lnr}	7.16	g g N^{-1}
k	1, 1.5, 2	unitless
O_i	21.3	kPa
SAI	1.5, 4	unitless
W	5	unitless

