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Sphagnum limits

Physiology, morphology and climate

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Abstract

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Sphagnum is the most important plant genus in terms of terrestrial carbon cycling. It and the habitats it creates store an equivalent of ~68% of the CO₂ in the atmosphere. The genus has little dispersal limitation and the mire habitats are functionally similar at global scales. *Sphagnum* species are limited by water deficit at local and biogeographic scales, but this alone is not sufficient to explain local and global scale species patterns. As *Sphagnum* shoots are long-lived they may be limited by stochastic periods of cold temperature. Within Europe, species are associated with climate gradients along north-south (cold-warm) and oceanic-continental (wet-dry) clines. Within mires, species are sorted along a moisture (hummock-hollow) gradient.

In this thesis I examined species responses to and recovery from freezing (I). I compared species with different water level niches in traits related to water management of individual shoots and colonies (II). Using distribution modelling of GBIF data, I estimated how different aspects of climate contributed to *Sphagnum* species distributions in Europe (III). Combining the approaches in papers II and III, I modelled the climatic distributions of the parapatric species *S. cuspidatum* and *S. lindbergii* and assessed how traits of water economy varied across the distribution boundary (IV).

Species responses to winter stress were largely allied to both their hydrological niche and geographic range. Generally, hollow species managed better than hummock species, but species from intermediate positions were less consistent in their response. Species associated with boreal regions were generally less affected than those from temperate regions. Hardening against low temperature was triggered by shorter days and cold nights. Cold temperatures during late autumn may be more important for *Sphagnum* limits than the minimum temperature during winter.

Water-related traits split the species into two groups; hollows species with large capitula and hummock species with small capitula. However, inter- and intra-specific trait variation and trait trends along the hydrological gradient were not necessarily the same at the shoot and canopy scale. Some trait correlations were common to all species. Canopy traits, which were emergent traits of colonies of shoots, had the strongest trait associations with the species position along the hummock-hollow gradient.

At the continental scale the distribution of most *Sphagnum* species could be successfully modelled by a combination of annual degree days and water balance and the degree of seasonality in these two variables. Individual species distributions were shaped more by the seasonality in degree days than in water balance.

Across the distributional border of *S. cuspidatum* and *S. lindbergii* divergence in the measured traits was mostly seen in the capitula indicating that limits to *Sphagnum* species are strongly linked to the functioning of the capitulum. Capitulum mass of both species was lower in sympatry than in allopatry, even though the measured values were similar. Canopy traits most strongly separated the species though did not change across the species boundaries.

In summary, *Sphagnum* species in general are limited by the availability of water. Low temperature, particularly during late autumn are probably decisive for the biogeographic limits and for the distribution of species along the hydrological gradient.

Keywords: *Sphagnum*, ecology, bryophyte, winter, species distribution models, low temperature, plant structure, water economy

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To Sarah, Beatrice and Marcus

List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I Campbell, C., Rydin, H. (2019) The effects of winter stress on *Sphagnum* L. species with contrasting macro- and micro-distributions *Journal of Bryology* :
<https://doi.org/10.1080/03736687.2019.1626167>
- II Campbell, C., Granath, G. and Rydin H. Structural traits of *Sphagnum*: Interrelationships and implications on water economy. (Manuscript)
- III Campbell, C., Granath, G. and Rydin H. Climatic drivers of *Sphagnum* distributions. (Manuscript)
- IV Campbell, C., Granath, G. and Rydin H. Trait variation across species distribution boundaries in *Sphagnum*. (Manuscript)

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Contents

Introduction.....	9
Mires and peatlands.....	9
<i>Sphagnum</i>	9
Origin and basic morphology	9
Water economy and ecology	9
Adaptations to cold climate	12
Dispersal, recruitment and the distribution of <i>Sphagnum</i> species	13
Aims of the thesis.....	15
Methods	16
<i>Sphagnum</i> and its physiological responses to winter stress (I)	16
Growth and mortality.....	17
Maximum photosynthetic capacity.....	17
<i>Sphagnum</i> morphology in relation to water economy (II and IV)	18
<i>Sphagnum</i> species distributions and climate (III and IV)	18
Results and Discussion	20
Mire surface temperature and responses to low temperature in <i>Sphagnum</i> (I).....	20
<i>Sphagnum</i> and winter stress (I)	22
<i>Water relations and morphology</i> (II).....	24
<i>Sphagnum</i> distributions (III)	27
<i>Sphagnum</i> traits across distribution boundaries (IV)	29
Conclusions.....	31
Vitmossans begränsningar: fysiologi, morfologi och klimat.....	32
Acknowledgements.....	35
References.....	36

Abbreviations

Variable (abbreviation)	Measurement (unit)
Shoot traits	
Capitulum mass (CPg)	Dry mass of capitula, top cm (g cm^{-1})
Stem mass (STg)	Dry mass per cm (g cm^{-1})
Fascicle density (nF)	Number of fascicles per cm of stem (cm^{-1})
Stem Leaf density (nS)	Number of stem leaves per cm of stem (cm^{-1})
Spreading branch length (Sbr)	Mean of 10 branch measurements (cm)
Pendent branch length (Pbr)	Mean of 10 branch measurements (cm)
Capitulum:stem mass ratio (C:S)	Capitulum dry mass/Stem dry mass
Canopy traits	
Capitulum density (N)	Numerical density (capitula cm^{-2})
Surface roughness (Ra)	Variance in height of canopy surface (cm)
Roughness Scale (Sr)	Unitless measure of distance between elements of Ra
Fractal dimension (Fd)	Unitless measure of self-repeating complexity
Bulk density capitula (CP_BD)	Mean capitulum dry mass \times capitulum density (g cm^{-3})
Bulk density stem section (ST_BD)	Mean stem dry mass \times stem density (g cm^{-3})

Introduction

Mires and peatlands

Species of the *Sphagnum* genus are the dominant plants of mires. Mires are active peatlands where a high water table slows the rate of decomposition of plant litter. High water tables result in low oxygen availability and low pH, leading to an accumulation of carbon rich peat. Non-tropical peatlands store 562 Gt of carbon, equivalent to ~68% of CO₂ in the atmosphere today (829 Gt) (Yu *et al.* 2010, Stocker *et al.* 2013). *Sphagnum* species are adapted to grow in these wetlands and their traits of high water holding capacity (up to 20x dry mass), recalcitrant litter, and cation exchange capacity actively promote peat formation. Hence they are keystone species of mires (Van Breemen 1995). Knowledge of the limits of *Sphagnum* is important to understand the changes that may occur in the face of a changing climate.

Sphagnum

Origin and basic morphology

Sphagnum are bryophytes, which are non-vascular, spore producing plants. The genus separated from other bryophytes about 400 million years ago and had a large diversification 5-50 million years ago (Shaw *et al.* 2019). Bryophytes transport the majority of their water externally, through an interconnected network of capillary pore spaces (Proctor 2008). However, unlike most bryophytes *Sphagnum* have evolved hyaline cells. These are large, dead cells that retain water for the photosynthetic chlorophyllose cells that are sandwiched between them.

Water economy and ecology

Each hyaline cell has a series of pores that allow for the flow of water into and out from the cell. The ability of the cell to retain water is determined by the menisci of these pores (Lewis 1988). Following capillary law the pore radii indicate that a capillary tube of equivalent size would transport to a height of 10 m (pressure equivalents of -100 cm H₂O or -100 KPa) (Hayward and Clymo 1982, Lewis 1988, Thompson and Waddington 2008). However, such

a pressure differential is met on all but the wettest of days (Hayward and Clymo 1982). Physiologically important volumes of water are maintained by the replacement of water lost through evaporation at the surface. In mires, this replacement comes most often from the sub-surface water table (Rydin and Jeglum 2013). The gross morphology of *Sphagnum* shoots and canopies (moss carpet) form an interconnected capillary network of pores which connect the growing tip to the water table below (Hayward and Clymo 1982).

How much water is available for an individual shoot is dependent on the individuals surrounding the shoot, i.e. on the moss canopy structure (Rydin 1986). Morphologies of *Sphagnum* related to water economy form two basic patterns; small shoots which form tightly packed colonies, and large shoots which form looser colonies (Elumeeva *et al.* 2011). These morphologies reflect two main trait associations in *Sphagnum* associated with fast and slow growth (Bengtsson 2019).

Sphagnum shoot growth is dictated by functioning of the top 1 cm of shoot. This part, known as the capitulum, is a whorl of young branches surrounding a primary meristem, where new branches and leaves are formed. Below this capitulum there is a secondary meristem where cell elongation causes the shoot to grow upwards (Ligrone and Duckett 1998). As the shoot elongates groups or fascicles of pendent and spreading branches are left behind along a stem, forming the bulk of the *Sphagnum* shoot. Functioning of both meristems requires a supply of water from the environment through the capillary network formed of overlapping shoots and branches.

Growth rate is the main determinant in the outcome of competition between *Sphagnum* species (Rydin 1993, 1997). A shoot's presence in a mire surface is dependent on it maintaining parity with the rates of growth of the surrounding shoots. Too fast, and it will be exposed, desiccate and stop growing, too slow and it will be out competed (Rydin 1993, Bien 2000). Species shoots occupy points above the water table where they can maintain a hydrological niche (Rydin 1985). Fast growing species such as *S. cuspidatum* grow close to the water table (in hollows) and slower growing species, such as *S. fuscum*, further away (in hummocks) (Bengtsson *et al.* 2016). The gradation between hollow and hummock has been split into four broad habitats (Sjörs 1950); pools, carpets, lawns and hummocks. Respectively these four occur in increasing distance from the water table and are related to the frequency of inundation. From near constantly in pools to never in hummocks. The habitats have different physical structures, as a consequence of the plant species from which they are formed. Pools and carpets are generally soft habitats, formed from loosely connected stems. Lawns and hummocks are firmer, formed from densely packed shoots.

The growth forms of the species create interstitial spaces that have varying potentials for capillary rise, keeping the capitulum moist and photosynthesizing. Capillary spaces are larger in species of hollows as water is freely avail-

able; meaning growth is less limited. These species typically have large capitula and fast rates of photosynthesis. Hummock species have slower growth rates but their litter has a slower rate of decomposition (Bengtsson *et al.* 2016). The subsequent build-up of peat results in a higher mire surface where only high capillarity species can survive (Van Breemen 1995). Typically, this environment favours a selection of species from the sections (subgenera) *Acutifolia* and *Sphagnum*. However, scattered shoots of species more typical of hollows may be present, such as *S. balticum*. *Sphagnum* shoots are notoriously plastic in their growth form. Small shoots of *S. balticum* mimic the typical growth form of *S. fuscum* and thus integrate into the surface matrix of shoots (Rydin 1986).

Bryophyte surfaces, including *Sphagnum*, lose water at rates dictated by the variation in their height at different scales (Hayward and Clymo 1983, Rice 2012). Most evaporation is a result of variation in height between shoots, but significant evaporation occurs at the scale of branches and leaves (Rice *et al.* 2001). Rice (2012) proposed that higher surface roughness represents a hazard for growth for shoots that are highly connected. Where shoot integration is important for transport, surface roughness must be low as the higher evaporation rate increases the chances a shoot will dry out. However, the amount of water surrounding a shoot affects the rates of gas diffusion and as a consequence, photosynthetic rate and growth. Comparing four species Schipperges and Rydin (1998) showed that *Sphagnum* had varying photosynthetic rates at high water content (above 1200% dry mass). Species maximum photosynthetic rates were found to be at water contents between 800 and 1000% dry mass. All species showed dramatic drops in photosynthesis below this 800% threshold. Low water availability and subsequent desiccation represents a hard limit to *Sphagnum* growth. Bragazza (2008) found during an extreme heatwave a combination of desiccation and high temperature resulted in a mass die-off of shoots in the Italian Alps. A combination of a long period of desiccation and high temperature can be hazardous to *Sphagnum*.

Growth in *Sphagnum* is temperature dependent. Increased temperature has been shown to affect the outcome of competition on its own (Breeuwer *et al.* 2008) and in combination with variation in the water table and available nitrogen (Robroek *et al.* 2007, Breeuwer *et al.* 2009). Haraguchi and Yamada (2011) found that photosynthesis increased at similar rates between 5 and 25 °C for five species. After which two species reached their photosynthetic peak at 30 °C and three at 35 °C, before all species had dramatic reductions at 40 °C. Temperatures in moist mire surfaces are unlikely to reach such high temperature as are set by the heat capacity of water and evaporation rates (Rydin 1984, Van der Molen and Wijmstra 1994). Dry mire surfaces in Scandinavia can reach temperatures above 40 °C depending on aspect (Rydin 1984). However such high temperatures are likely short lived and the dry shoots themselves are likely dormant. *Sphagnum* species do have the capability of func-

tioning at high, 40 °C, temperature (Lange 1973). Therefore, the highest temperatures that continually moist mire surfaces reach, may not be limiting to *Sphagnum* as they fall well within the physiological limits of the genus. Despite *Sphagnum* biomass being greater at high latitude, the effects of low temperature on the species have been under investigated. This has taken on new interest as recent evidence suggests that intra-generic clades first arose in the northern hemisphere at high latitudes before range expansion and further diversification into the tropics and southern hemisphere (Shaw *et al.* 2019).

Adaptations to cold climate

In northern Europe, the limits of large groups of plants are described by the mean temperature of the coldest month (Dahl and Birks 1998). Physiologically, this limit is related to the frost sensitivity of the species. Cold periods affect growth and survival of individuals and form their populations and species limits. Severe periods of cold which have long lasting effects on species populations and subsequent distributions may occur rarely or irregularly (Woodward 1990).

Freezing injury in plants comes from the formation of extracellular ice. Ice formation on the outside of cells creates a water potential that may dehydrate the cell, and this is probably the main cause of freezing injury. As ice crystals get larger they may cause mechanical tears in the cell membrane by physically breaking them. The precise mechanisms of frost survival are unknown, however to survive freezing plants must increase the cryostability of their cell membranes and decrease cell water potentials (Sakai and Larcher 1987, Xin and Browse 2000, Kawamura and Uemura 2014). Such biochemical changes are shared with mechanisms of desiccation tolerance.

Bryophytes in general are adapted to surviving long periods of desiccation (Proctor *et al.* 2007). As water loss is not directly controlled by bryophytes, periods of time without water are inevitable. Bryophytes survive such periods by ceasing metabolic activity and limiting further cell water loss (Proctor 2008). *Sphagnum* has been shown to be drought tolerant, provided that repeated partial desiccation occurs beforehand (Hájek and Vicherová 2014). Repeated freeze-thaw events during autumn will result in short periods where *Sphagnum* cells dry out. Extracellular ice lowers the water potential outside the cell during the night. After sunrise this ice will melt returning cells to full turgor. Hájek and Vicherová (2014) found that desiccation tolerance increased in several *Sphagnum* species in October and November. Such changes in desiccation tolerance are mirrored by biochemical changes in *Sphagnum*.

Seasonal changes in bryophyte sugar concentration and its relationship to frost tolerance have been recorded (Rütten and Santarius 1992, 1993). In *Sphagnum* seasonal changes in both concentration and composition of lipids have been detected, along with a slowing of growth (Karunen and Salin 1982).

Li and Glime (1991) showed that shorter days (below 10 h of day light) resulted in both *S. magellanicum* and *S. papillosum* decreasing and even stopping growth.

During autumn, day-length decreases and there is a drop in night-time temperature. Both of these changes trigger cold acclimation and in combination result in maximum hardiness of a plant (Sakai and Larcher 1987). Comparisons of bryophytes showed that many species are naturally tolerant of very low temperature (Dilks and Proctor 1975, Segreto *et al.* 2010), but also indicate that *Sphagnum* is not (Balagurova *et al.* 1996, Segreto *et al.* 2010).

Tests of low temperature survival in *Sphagnum* have focussed on cellular damage (Buchner and Neuner 2010), quantified damage immediately after temperature treatment (Balagurova *et al.* 1996) or studied plants that were subjected to extreme temperature (-80 °C) (Segreto *et al.* 2010). Survival after such events may not be solely dependent on the temperature reached, but also the environment prior to, and after the treatment.

The lack of direct control of their water economy means that prior to freezing, bryophytes and particularly *Sphagnum* may be surrounded by large amounts of water. Lenné *et al.* (2010) showed that the common bryophyte *Ceratodon purpureus* is desiccated when frozen as an adaption to surviving low temperature. Ice nucleation on the surface removed water from the moss. Artificially increasing water content prior to freezing resulted in internal ice formation. Moffett (2015) showed that induced ice nucleation was common in both mosses and liverworts. As *Sphagnum* species have different realised hydrological niche position, it is probable that the combined effects of water content and low temperature may play a role in species competitive hierarchies and resultant distributions along that gradient.

Dispersal, recruitment and the distribution of *Sphagnum* species

Despite being ecologically specialised, many *Sphagnum* species are common across the northern hemisphere, a consequence of their effective dispersal. Long-distance dispersal in *Sphagnum* is by spores, which are released explosively from the capsules of the sporophyte (Sundberg 2010, Whitaker and Edwards 2010). Spores are brought up to higher altitude by the wind, and can then have an effective dispersal range of several hundred kilometres (Sundberg 2013). This efficient dispersal mechanism is often reflected in the population genetics, where frequently spore-producing species can exhibit higher genetic diversity between patches in a mire than between mires 100s of km apart (Mikulášková *et al.* 2015). Such genetic patterns are a result of recruitment and *Sphagnum* shoot longevity

Sphagnum shoots are long lived. Evidence from Europe and Hawaii suggest that within a stable habitat the same individual may occupy the space for 100s if not 1000s of years (Rydin and Barber 2001, Karlin *et al.* 2012).

Changes in mire *Sphagnum* composition do occur but are linked to large environmental shifts in climate and/or hydrology (Rydin and Jeglum 2013). Large scale community shifts rarely occur spontaneously, as development of new plants from spores does not occur on living *Sphagnum* (Clymo and Duckett 1986). Consequently founder effects of suitable habitat is a strong determinant of community composition. However, continued presence in a habitat is dependent on the species being able to compete through normal and catastrophic conditions (Clymo and Hayward 1982, Chesson and Huntly 1997). The consequences of these processes are the limits of *Sphagnum* species distributions at micro and macro scales.

Sphagnum's geographical distributions are a consequence of large geographic and climatic barriers. Kyrkjeeide *et al.* (2016) showed that genetic structuring within several common *Sphagnum* species was consistent with limitation by habitat availability, as well as dispersal barriers caused by landmasses, oceans and wind direction. Landmasses proved to be the strongest barrier, with many species occurring on both sides of the Atlantic and/or the Bering strait while being absent from the opposing side of the continents.

In Europe few physical barriers exist of an appreciable scale to limit spore dispersal. Yet *Sphagnum* species show biogeographic affinities (Daniels and Eddy 1990, Flatberg 2013). *Sphagnum* species are associated with north-south (cold-warm) and oceanic-continental (humid-dry) clines. Evidence from Canada shows that one of these limits is water availability. Gignac *et al.* (2000) and, Oke and Hager (2017) both show that peatlands and *Sphagnum* do not occur where precipitation minus potential evapotranspiration was < -500 mm y^{-1} . This represents a hard climatic limit for the genus and subsequent habitats but does not explain species limits and distributions.

Aims of the thesis

The aims of this thesis is to evaluate the limits to *Sphagnum* at a local (microtopography) and macro scales (continental).

Specifically I addressed the following questions:

1. What are the eco-physiological effects of winter stress (low temperature and high water table) on species with different biogeographical and hydrological niches? (I)
2. How do traits of water conductance at the shoot and canopy level change inter- and intra-specifically across the *Sphagnum* species and to what extent do they reflect microhabitat and water balance? (II)
3. What climate variables, temperature or water balance, affect species distribution patterns at the continental level in *Sphagnum*? (III)
4. How do traits relevant for water economy change across the border of the distributional limits of parapatric bryophytes? (IV)

Methods

Sphagnum and its physiological responses to winter stress (I)

In several experiments I tested the responses of up to nine species of *Sphagnum* given different hardening regimes and different types of winter stress. All species involved can be abundant on ombrotrophic mires in Europe. They comprised species representative of different positions along the hummock-hollow gradient as well as being species with different biogeo-graphical centres of distribution.

To examine temperature differences between months, sites, hummocks-hollows, I recorded near surface temperature at the mires Kulflyten and Ryggmossen, eastern Sweden from July 2014 to August 2015. Temperatures recorded covered a micro-topographic height range of 40 cm. As my interest was in the extremes of temperature I compared the maxima and minima of the warmest and coldest months in relation to height above the mean water table between the two sites.

The first experiment tested species innate ability to withstand cold temperatures for different periods of time. Shoots from seven species were kept for a week at 20 °C with ample water to remove any hardening. They were then placed in climate chambers with a supply of water for 1, 7, 14 and 26 days and were maintained at a steady temperature of 20, 5, -5 and -10 °C.

The second experiment tested the rates at which species hardened to winter stress. A total nine species were kept at a constant 20 °C for a month to de-harden them. They were then kept in a growth chamber at 5 °C day and -1 °C night. Each day five shoots of each species were removed and placed in sealed tubes and frozen in the dark for 48 h at -5 °C.

The third experiment tested species low temperature survival once hardened with different day-lengths and night temperature. Shoots from six species were kept for a month under different hardening regimes that were fully factorialised day length and night temperature treatment of 12 h vs 6 h and constant 5 °C vs -1 °C at night. These shoots were then treated at 5, -5, -10 and -18 °C for 48 h before being allowed to recover at 20 °C for 28 days.

I measured three aspects of *Sphagnum*'s physiological response to winter stress: Growth, mortality and maximum photosynthetic capacity.

Growth and mortality

I defined growth as the difference in shoot length between the start and the end of the experiments. As growth is not possible in freezing conditions, I standardised this measurement by dividing by the total number of days a shoot had been in above 0 °C conditions. I recorded a shoot as being dead if it had lost all colour, or if it lost a significant number of leaves and branches after being pressed lightly with a finger.

Maximum photosynthetic capacity

I inferred photosynthetic capacity using measurements of chlorophyll fluorescence. Photosynthesis is a sequential process comprising a set of light-dependent reactions, photosystem II (PSII), and light-independent reactions, photosystem I (PSI). When energy in the form of light is absorbed by chlorophyll it can be used to drive photosynthesis, but it is also re-emitted as heat or light (fluorescence). These three processes occur in competition in such a way that information on one provides information regarding the other two (Murchie and Lawson 2013).

Measuring chlorophyll fluorescence is done by first keeping the plants in the dark for at least 20 minutes. Plants are then exposed to light of differing intensities and for different periods of time depending on what fluorescence variable is measured (see Murchie and Lawson 2013). I measured maximal photosynthetic efficiency (F_v/F_m) which has been shown to be a good proxy for plant stress.

Measurement of F_v/F_m is done whilst the plants remain in the dark. A pulse-modulated fluorometer is used to measure the amount of light being fluoresced (F_0). It then flashes a short, very intense burst of light and immediately after again measures the amount then being fluoresced (F_m). The proportional difference between the two measurements is the maximal photosynthetic efficiency $((F_m - F_0)/F_m)$. This variable has a theoretical range of 0-1 however, typical unstressed plants return values of ~0.83, and stressed plants have lower values than this.

Plants are adaptable, and measurements of plant stress are context dependent. Values of F_v/F_m will be influenced by several different factors including temperature and length of time since treatment. Lovelock *et al.* (1995) showed that mosses regain pre-treatment F_v/F_m values after 12 h recovery. As my interest was in damage, I measured F_v/F_m 24 hours after the plants had been removed from the treatment chambers and had been kept with ample supplies of water at 20 °C. Any reduction in F_v/F_m was indicative of lasting damage of the temperature treatment.

Sphagnum morphology in relation to water economy (II and IV)

I collected data on 13 morphological traits related to water maintenance from 8 common boreal bog species (*S. balticum*, *S. cuspidatum*, *S. fuscum*, *S. lindbergii*, *S. magellanicum*, *S. majus*, *S. rubellum* and *S. tenellum*). Plants were collected on the open-bog plateau at the site Kulflyten (II). These same morphological traits were then measured in *S. cuspidatum* and *S. lindbergii* at 9 other sites (IV). All traits were measured within a 69-mm diameter sample.

Traits were divided into measurements at two scales; shoot traits and canopy traits (see Abbreviations). Shoot traits were measured on a single shoot and comprised capitulum mass, stem mass, mean length of longest spreading and pendent branches from ten fascicles, density of fascicles, and density of stem leaves. Canopy traits were measured only with groups of shoots. They included shoot density, capitulum and stem bulk density, and three surface form traits (surface roughness, roughness scale and fractal dimension) described in Rice *et al.* (2001). Surface form traits were measured using photogrammetry.

Photogrammetry uses digital photographs taken from multiple locations. The photographs along with the collected metadata are used to digitally recreate objects in three dimensions. Associated with each digital photograph are metadata files that contain information about the camera settings used when taking a photograph, such as the focal length. By finding common features between photographs the relative distances between structural features can be found and a 3-dimensional point cloud of features created. I used a rasterised version of this point cloud to create semivariogram models of surface variation in the samples. From these semivariograms I calculated the surface variables surface roughness, roughness scale and fractal dimension following Rice *et al.* (2001). Surface roughness represents the mean difference between height elements (peaks and troughs) of a surface. Roughness scale is the mean distance between those height elements as a proportion of height. Fractal dimension is equivalent to the rate of change in semivariance at very small distances. These three measurements represent variation in height at the scale of shoot, branch and leaf Rice *et al.* (2001).

Sphagnum species distributions and climate (III and IV)

I used species distribution modelling to quantify species relationships with climatic variables. Specifically I used maximum entropy modelling as implemented by MaxEnt ver 3.4.1. (Phillips *et al.*, 2017).

MaxEnt is a machine learning algorithm that has been shown to have amongst the best predictive powers for species distribution modelling in comparison to other modelling frameworks (Wisz *et al.* 2008). It uses presence /

background data to identify the relative occurrence rate of a species in relation to environmental covariates (Elith *et al.* 2011).

Species record data were downloaded from Arctoa (<http://arctoa.ru/Flora/basa.php>), Biocase (<http://www.biocase.org/>), Gbif (Occdownload Gbif.Org, 2017) and the Finnish Biodiversity Information Facility (<https://laji.fi/en>). In addition I supplemented with records from the scientific literature. I followed Hodgetts (2015) for taxonomy with the notable addition of *S. beothuk* which has been widely recorded now in the British Isles, Ireland and Norway. I treated *S. magellanicum* as a single species as the split into *S. divinum* and *S. medium* is recent, and old recordings are not assigned to either of them (Hassel *et al.* 2018).

Plant species are limited by water availability and the temperature regime (Guisan and Thuiller 2005). As a measure of water availability, I calculated the difference between the precipitation and potential evapotranspiration per month. Potential evapotranspiration is a predicted measure of evaporation over a standardised vegetation surface (Abteu and Melesse 2013). It gives an indication of direct rates of water loss to the atmosphere.

I calculated degree-days per month as a measure of the temperature regime of the region. Degree-days were calculated as the mean of the maximum and minimum of a month multiplied by the days in that month. The scale indicates both degree and duration of temperature in a region.

I summed the per-month values to give an annual value and calculated the standard deviation as a measure of climate variation. These were termed annual degree-days, annual water balance, degree-day seasonality and water balance seasonality.

Results and Discussion

Mire surface temperature and responses to low temperature in *Sphagnum* (I)

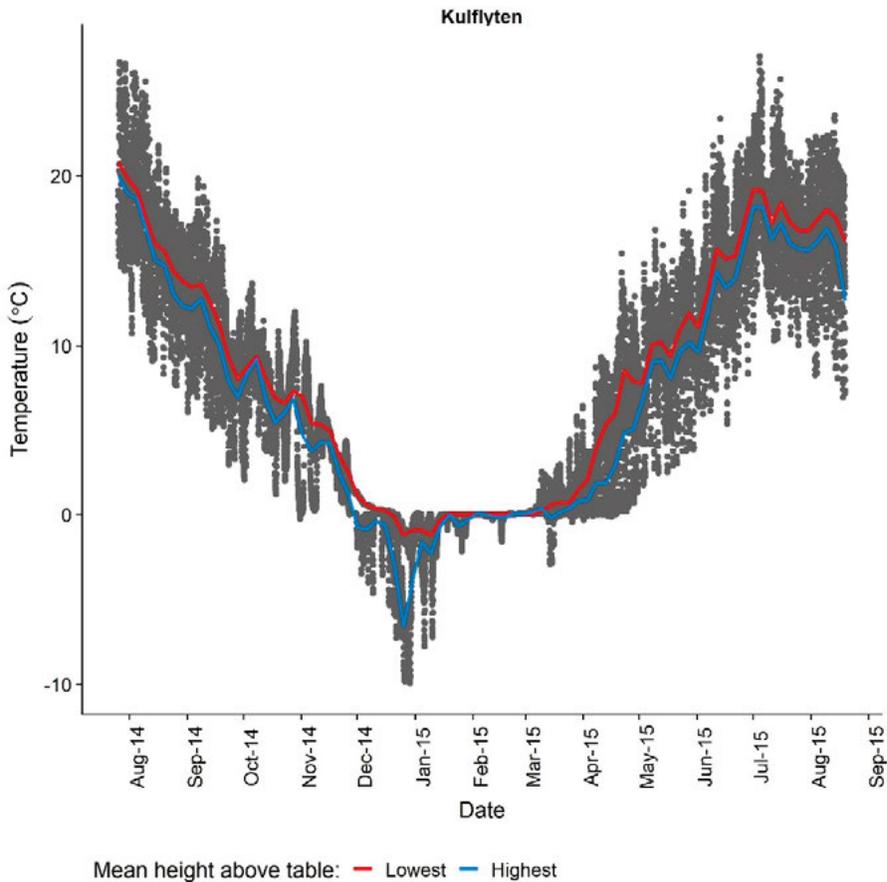


Figure 1. Temperature recorded at 2 cm below the surface at Kulflyten (N:59.90, E:15.82) at the highest and lowest points in the mire surface.

At both Ryggmossen and Kulflyten the highest temperature was recorded in July at the lowest points in the hummock-hollow gradient. The coldest temperature was at the highest hummock points during December. Hummocks

were consistently colder than hollows. Air temperature is usually highest during July and coldest during January or February. Mires in boreal regions usually are covered in an insulating layer of snow over much of the winter (Soneson 1969). The result is that the coldest temperature that *Sphagnum* experience is during late autumn and early winter, before significant snowfall (Figure 1).

Minimum temperature per month was almost consistently 2 °C lower at Kulflyten than at Ryggmossen. In both mean and maximum temperature the sites were very similar. These two sites are located on each side of an important climatic transition zone (boreal vs nemoral-boreal) where many species, including *Sphagnum* (see study III), have their distribution limit (Dahl and Birks 1998; Sjörs 1999). Comparison of my results during the summer months with similar temperature data from mires in England (Clymo and Hayward 1982), Ireland (Van der Molen and Wijnstra 1994) and Siberia (Dyukarev *et al.* 2009) show a similarity in mean temperature between sites even though they are 1000s of km distant.

In summer, the hummocks were consistently colder than the lower parts. Mire surface temperature is a consequence of heat capacity, thermal conductivity and thermal diffusivity, which vary with water content (Van der Molen and Wijnstra, 1994). When a mire is fully wetted hummocks have lower water contents than the hollows, with stored heat being lost to the atmosphere through evaporation. But after a dry period, it is particularly the hollow species that dry out, and this is reflected by the high temperatures reached in the lower parts of the mires in July. Provided mire surfaces remain wet, temperature at the surface will not exceed those suitable for *Sphagnum* growth and survival during summer (Rydin, 1984).

Sphagnum and winter stress (I)

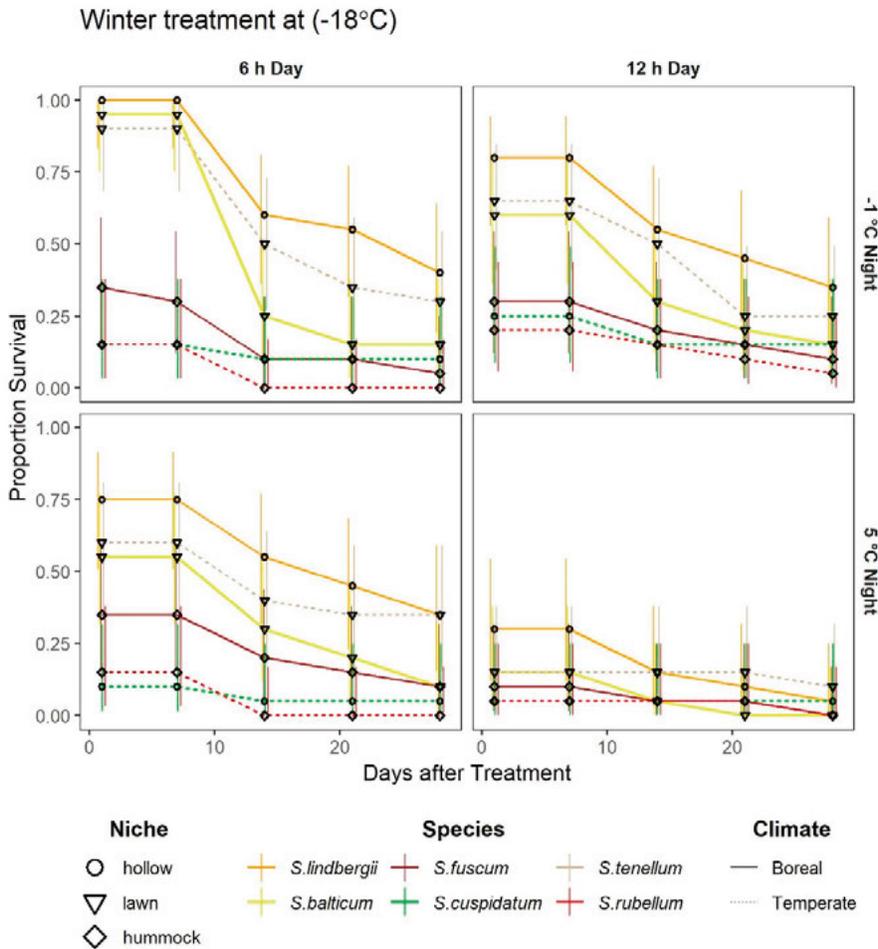


Figure 2. The survival of six species of *Sphagnum* with differing hydrological niches and climatic distributions treated with -18 °C for two days. Shoots were subjected to full factorialised pre-treatments of short day (6 h), long day (12h) and cold nights (-1 °C), warm nights (5 °C) for 1 month. After the freezing treatment shoots were kept at 20 °C, and survival was checked after 1, 7, 14, 21 and 28 days.

Rapid hardening to freezing stress is important for *Sphagnum* species to survive winter, particularly as the lowest biologically relevant temperature may occur in late autumn. Unhardened plants had lower F_v/F_m values and had slower growth rates after treatment with low temperatures than hardened plants. Species had varying degrees of innate (unhardened) frost tolerance. Surprisingly, *S. lindbergii* had lower F_v/F_m values than *S. cuspidatum* indicating that in its unhardened state this boreal species was not tolerant of cold temperature.

Hardening was promoted by short days and cold nights; plants with such pre-treatments could better survive freezing at -18 °C (Figure 2). Separately these treatments conferred a similar degree of frost tolerance, but when applied together *Sphagnum* species had a greater proportion of shoots survive.

Once hardened, species responses to freezing were indicative of, but did not perfectly match their biogeographical distribution and their position along the hydrological gradient. *S. balticum*, *S. lindbergii* and *S. tenellum* had higher rates of survival than *S. cuspidatum*, *S. fuscum* and *S. rubellum* when treated with -18 °C (Figure 2). *S. lindbergii* and *S. cuspidatum* are both competitors in pools, *S. lindbergii* being the boreal counterpart. Species associated with pools generally had higher values of F_v/F_m , higher survival and less impacted growth than species of hummocks from the same biogeographic region. Similarly, species of boreal pools and hummocks were affected less than their temperate counterparts. This pattern did not necessarily hold true for species of the lawn and carpets, where there was no clear difference between species of different biogeographic regions.

In testing species rates of hardening, I found that pool and hummock species reacted quickly to the pre-treatment, whereas lawn and carpet species did not. These species took the longest to harden, and were impacted by the treatment the most. There was some degree of biogeographic patterning as the most boreal species, *S. balticum*, was affected the least, followed by *S. papillosum* and *S. tenellum* and finally *S. magellanicum*.

Across all experiments, once hardened hummock and pool species were consistent in their responses. Species from lawns and carpets were not. I propose that as pools can dry out during summer and hummocks cool quickly during winter species of these niches are adapted to acquiring desiccation tolerance quickly. The lawn and carpet habitats fall between these environments. Species of this intermediate zone have been shown to grow and shrink in their coverage as the conditions change from year to year (Rydin 1993). This variation in environment allows species with adaptations favouring different conditions to co-exist. Winter stresses are another axis of variation for *Sphagnum* species.

My results support the hypothesis that species ability to withstand low temperatures structure their distributions. The twin winter stresses of low temperature in combination with high water content may play a strong role in structuring niche partitioning along the hydrological gradient.

Water relations and morphology (II)

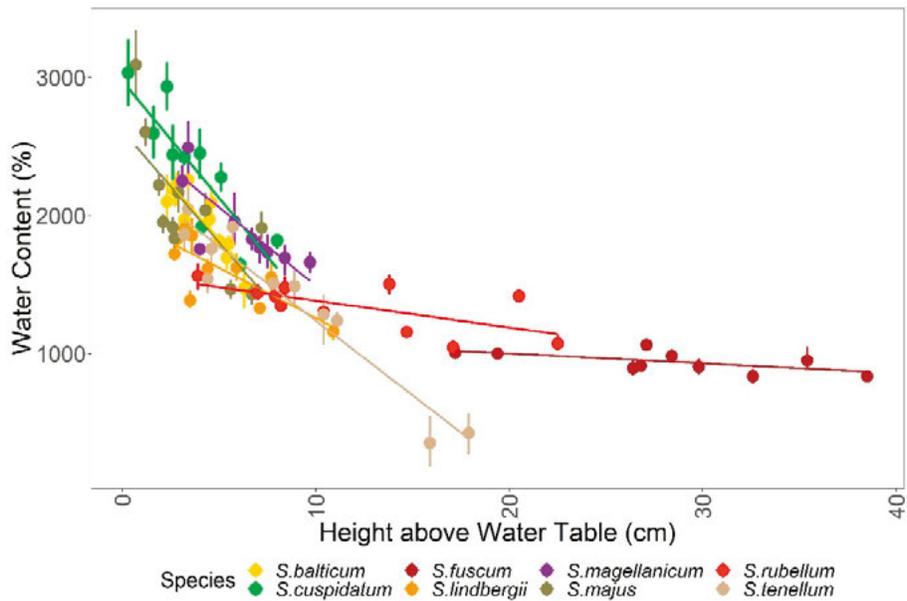


Figure 3. Relationship of gravimetric water content and Height above Water Table for eight species of *Sphagnum*. Lines are fitted linear regressions from a mixed model. Error bars are 1 SEM for each sample (n=5).

There was a negative relationship between height above the water table and water content in the field for all species (Figure 3), but the effect varied between species. Species appearing mostly below 10 cm height above the water table showed a strong decrease in water content as height above the water table increased. *S. fuscum* and *S. rubellum* mostly occurred well above 10 cm and their water content was almost unaffected by water level.

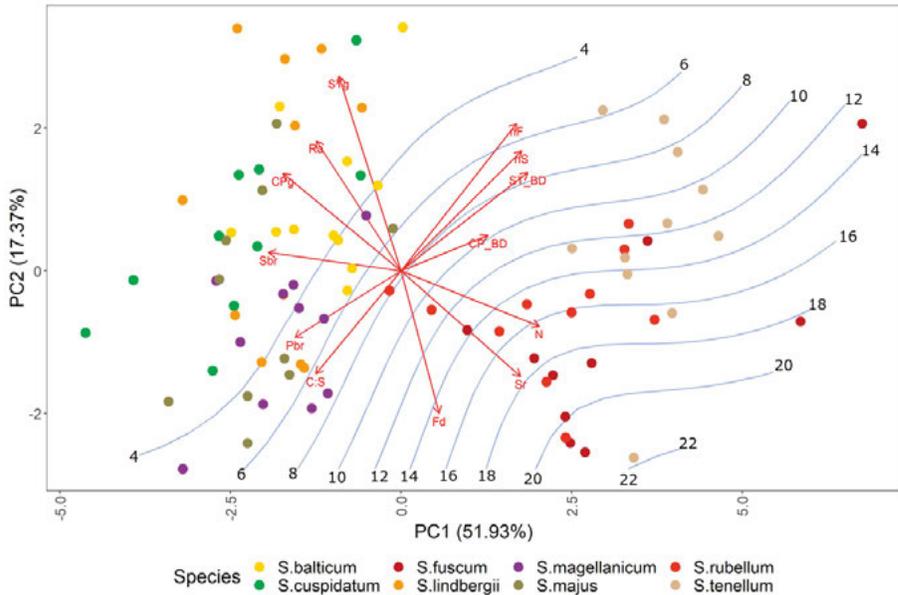


Figure 4. Principal Components Analysis of six canopy traits and seven shoot traits for monospecific stands of eight species of *Sphagnum*. Contour lines are the result of GAM surface fit of height above mean water table and the first two axes. See Abbreviations for trait definitions.

Species formed two groups in trait space (Figure 4). These groups conformed to a division between species which had samples >10 cm above the mean water table (hummock group) and those that grew lower (hollow group). (Lamentowicz *et al.* 2019) suggest a tipping point for mire species of wet to dry habitats at 11.7 cm, close to my identified 10 cm limit. The traits that were most strongly allied to height above the water table were the canopy traits: Shoot density, surface roughness (Ra) and roughness scale (Sr). These were closely followed by capitulum mass (CPg) and spreading branch length (Sbr). Pendant branch length, number of fascicles and stem leaves, and capitulum and stem bulk density were not strongly associated with the mean water table gradient. These results are in line with previous research showing that smooth aggregations of dense colonies lose water at a slow rate and explain the separation between the two groups identified here (Elumeeva *et al.* (2011)).

Trait trends across the hydrological gradient were often different between and within species and few trait correlations were common to all species. The extreme example was *S. tenellum*. This species occurred much higher above than mean water table than its water content to water table relationship would predict. Its canopy architecture was such that it reduced water loss to the environment by having highly numerous, densely packed shoots with a very smooth surface. *S. tenellum* has a rather high photosynthetic capacity (Bengtsson *et al.* 2016) and is desiccation tolerant (Økland 1990). To summarise these traits combinations allow it to utilise transitory patches in peatland surfaces.

Though at competitive equilibrium it is found closer to the water table as it will be outcompeted from transitory patches (Rydin 1986).

Intraspecific trait responses to height above the mean water table were more variable in hollow species than hummock species. As water is freely available for much of the year in hollows, growth is less limited. Many species had longer branch lengths at higher positions above the mean water table. Longer pendent branches have been cited as being important for water transport by several authors (Green 1968, Økland 1990, Såstad *et al.* 1999). Surprisingly there was no change in fascicle density (which is another trait that has been associated with water transport) with height above the mean water table. *Sphagnum* species forms are aptly suited to the conditions in which they can form monospecific patches and are more strongly limited by water loss than by traits of water transport.

Sphagnum distributions (III)

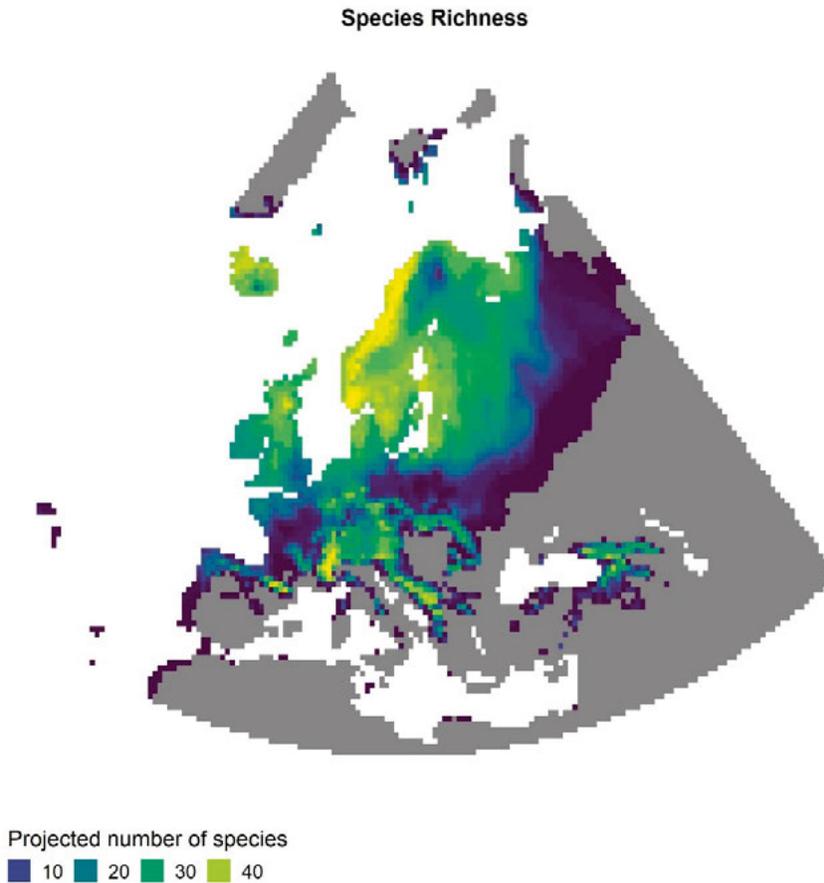


Figure 5. Projected *Sphagnum* species richness for the European continent. Species richness is projected from a stack of rasterised MaxEnt projections turned into presence absence.

Sphagnum species are concentrated to the north and west of Europe. *Sphagnum* species richness is highest around the north Atlantic coast and the Baltic region. Further south favourable climate is associated with mountain ranges, particularly the Carpathians, Caucasus, Dinaric alps, Pyrenees and the western Alps (Figure 5).

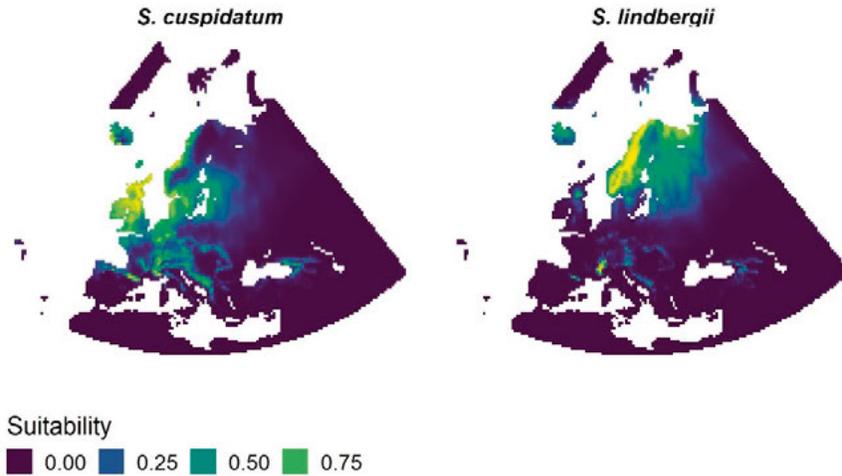


Figure 6. Projected climatic suitability for *S. cuspidatum* and *S. lindbergii* across Europe at a grid cell size of 50×50 km.

Reasonable projections of *Sphagnum* distributions could be made using the climatic variables that are linked to *Sphagnum* performance (Figure 6). *Sphagnum* as a group were bounded between values of annual degree-days of -5000 $^{\circ}\text{C y}^{-1}$ and 5000 $^{\circ}\text{C y}^{-1}$, but species differences were more obvious in degree-day seasonality. In these high latitudes degree-day seasonality is driven more by the minimum than the maximum temperature, indicating that frost tolerance can be a limitation for some species, which is in line with the results found in study I.

For most species climatic suitability increased above a water balance >-500 mm y^{-1} . This value has been suggested as a limit for peatlands and *Sphagnum* in Canada (Gignac *et al.* 2000, Oke and Hager 2017) and is a hard limit for *Sphagnum*, and by extension, high latitude peatlands. Exceptions were rare and included species with restricted distributions, for example *S. angermanicum* and *S. skyense*. These species may not be filling their fundamental climatic niche.

Water balance and available water are likely the main climatic factors affecting *Sphagnum* species presence in general. However, variation in temperature over a year better separated *Sphagnum* species in general.

Sphagnum traits across distribution boundaries (IV)

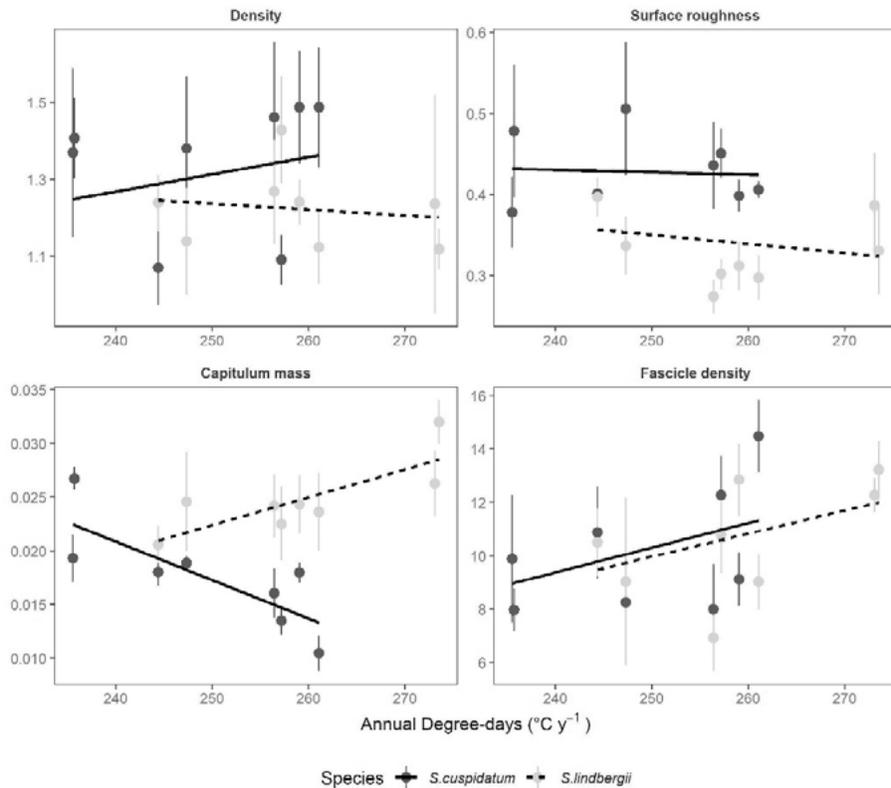


Figure 7. Responses to annual degree-days in shoot density (cm^{-2}), surface roughness (cm) capitulum mass (g) and fascicle density (cm^{-1}) for *S. cuspidatum* (black points, solid line) and *S. lindbergii* (grey points, dotted line) at ten sites in Sweden.

In Sweden *S. cuspidatum* is replaced by *S. lindbergii* towards the north (Figure 6). The overlapping zone is around the *limes norrlandicus* (the border between the boreo-nemoral and the southern boreal and examined in study I; Sjörs 1999), a limit where many temperate species reach their northern limits. As degree-day seasonality increased, the climatic suitability for *S. cuspidatum* dropped markedly whereas it remained high for *S. lindbergii*. This implies that *S. cuspidatum* is limited by variation in degree-days, which, as stated above, in boreal regions is most likely a result of temperature minima.

Trait responses in the two species were a mixture of species specific, environmentally controlled, an interaction of the two or no structure at all. Surprisingly, surface roughness, roughness scale (Figure 7) and fractal dimension (the three surface traits) were the most species specific traits. *S. cuspidatum* had greater surface roughness than *S. lindbergii* indicating faster rates of evaporation (Rice *et al.* 2001).

Fascicle density and stem leaf density were strongly associated with the environmental variables but with little difference between the species. Growth and competition in *Sphagnum* is dependent on maintaining the same height as neighbouring shoots (Rydin 1985). Growth is a result of stem elongation which here is recorded in the densities of fascicles and stem leaves (Ligrone and Duckett 1998). Since the densities are higher in the warmer climate where evaporation is higher, it is likely that this is a response to lower water deficit. The similar responses in the two species, and the tight link to climate show that growth in *Sphagnum* is strongly linked to climate.

For both species, capitulum mass decreased away from their distribution centres. *S. cuspidatum* was smaller further north and *S. lindbergii* further south. As production occurs in the capitula, it is interesting that this trait is greatly affected towards the edge of a species range. In *S. cuspidatum* I hypothesise that this is a result of low winter temperature affecting capitulum function. *S. lindbergii*'s lighter capitula and stem are possibly a result of higher linear growth rates and competition in the warmer south. Overshadowed shoots of *Sphagnum* grow taller, but smaller to prevent their being lost from the *Sphagnum* surface (Rydin 1995)

Conclusions

I found evidence that adaption to low temperature during autumn and early winter were important for species differentiation at local (within mire) and continental scales. Northern distribution limits for some species may be the consequence of rare low temperature events in the late autumn, rather than extremely low winter temperature (I and III).

Regulation of water loss rather than water transport, shapes the distribution of *Sphagnum* within a mire. Emergent canopy traits that decreased surface evaporation were important for hummock species, whereas larger trait variation is possible in the hollows (II). These traits also strongly separated *S. cuspidatum* and *S. lindbergii* across their distributional border (IV).

Water is key for the presence of *Sphagnum* (III). I found that *Sphagnum* presence in Europe occurred at similar values for *Sphagnum* presence in Canada, indicating a global limit for the dominance of *Sphagnum* and the presence of peatlands. Species distributional limits are filtered by the effect of low winter temperatures (I, III and IV). It is the combined effect of low temperature and water use that differentiate species niches at the local level (I and II),

Vitmossans begränsningar: fysiologi, morfologi och klimat

Myrar är torvbildande våtmarker och delas i in mossar och kärr. Många av Europas nuvarande myrar bildades strax efter den senaste istiden, det vill säga för ungefär 10 000 år sedan, men kan dock vara markant äldre där omständigheterna har varit gynnsamma. Torvmarkerna i Filippi, Grekland, till exempel, bildades redan för 700 000 år sedan. För att räknas som torvmark ska marken täckas av minst 25 cm torv, en kolrik jordart som består av ofullständigt nedbrutna växter. Det finns mer kol lagrat i torvmark än i världens samtliga skogar. Torv bildas aktivt på våtmark där en hög grundvattennivå leder till en miljö med en tillräckligt låg syrgasnivå för att förhindra att växterna bryts ner helt.

För 8 000 år sedan ökade antalet myrar rejält under den så kallade atlantiska perioden. Då var klimatet varmare och regnigare än idag, vilket gynnade bildningen av torv och tillväxten av vitmossa (*Sphagnum*), den dominerande växten i dessa miljöer.

Marken på mossar och i de flesta kärr täcks av vitmossor på det norra halvklotet, och vitmossor är avgörande för att torvmarkerna ska bibehållas. Vitmossorna kan hålla en vattenhalt över tjugo gånger sin egen vikt, och kan också sänka vattnets pH. Torvbildningen gynnas av låg syrehalt (som effekt av en ständig hög grundvattennivå), i kombination med en låg pH. Förutsatt att klimatet och miljön håller sig inom de gränser som gynnar vitmossans tillväxt, är myrar väldigt stabila livsmiljöer.

Vitmossor har dock begränsningar i vilka miljöer de kan växa. Av de gränser som forskningen känner till är flera kopplade till förekomst och transport av vatten. Upptaget av det vatten som behövs för att vitmossan ska kunna växa sker, som hos andra mossarter, utanpå växten. Vitmossans blad är bara ett cellager tjockt och består av levande celler omgivna av stora, vattenfyllda döda celler.

Vitmossans topp kan vara upp till 50 cm ovanför närmaste vattenkälla, i regel myrens grundvatten. Vitmossans grenar, blad, stammar och skott överlappar på ett sätt som gör att små håligheter bildas som då genom vattnets ytspänning och kapillärtryck gör det möjligt att dra upp vatten från grundvattnet ända upp till skottets spets. Olika arter har olika strukturer som bildar hålrum av olika storlekar. Arter med större håligheter växer snabbare men har inte förmågan att transportera vatten högt. Snabbväxande arter kan

överskugga långsamma arter, och tillväxthastigheten begränsas av den tillgängliga vattenmängden. Resultatet blir då att en arts förmåga att växa på en myr begränsas av hur pass högt de kan transportera vatten, vilket i sig påverkas av artens morfologi.

Där vitmossor har flyttats från låg position (hölja) till en hög position (tuva) inom en myr, har de inte överlevt. Men växter som har flyttats från tuva till hölja har överlevt och har så småningom vunnit mark efter flera år. En art kan inte växa på en nivå som är högre än sin vanliga livsmiljö, men har möjlighet att växa på lägre nivå.

Klimatet förändras starkt med latitud och longitud i Europa. Klimatfaktorer, i synnerhet låg temperatur eller vattenbrist, begränsar spridningen av kärlevväxter och insekter, men i nuläget vet man lite om vilka faktorer som begränsar olika vitmossarters utbredning. Flera forskare har undersökt vad som händer med vitmossor vid olika temperatur, men det har saknats forskning om hur vinterförhållanden, i synnerhet frost, påverkar vitmossorna ekologiskt. Vitmossans sporer kan färdas hundratals kilometer med hjälp av vinden. Varje spor kan bilda en ny mossa, men olika arter förekommer ändå i olika regioner. Det har visats att hav, berg och förhärskande vindriktningar kan hindra sporspridningen, men inga av dessa faktorer begränsar vitmossornas utbredning i Europa.

I min avhandling undersöker jag vitmossans begränsningar vad gäller låga temperaturer i kombination med hög fuktighet. Vidare tittar jag på hur såväl tillgång till vatten som klimat påverkar vitmossors utbredning inom myren och på kontinental skala.

I den första artikeln studerade jag vad som händer med vitmossan under vintern. Under både hösten och vintern sjunker temperaturen i myren och grundvattennivån stiger. I nordliga och högt belägna regioner kan marken täckas av djup snö under längre perioder. Jag mätte yttemperaturen i två myrar och kom fram till att deras minimumtemperatur skilde sig mest från varandra under tidiga vintern (innan myren täckts av snö). Eftersom vitmossans förmåga att överleva kan påverkas av frost, utforskade jag flera vitmossarters förmåga att tåla låga temperaturer. Jag samlade olika arter som växer i olika delar av myren (från tuva till hölja) och som har olika utbredning i Europa. De vinterhärdades under höstliknande förhållanden några veckor innan de sedan utsattes för olika vinterbehandlingar. Jag fann att korta dagar och låg nattetemperatur kan förbereda vitmossan för minusgrader och att sammantaget var det dessa faktorer som bidrog mest till frosttolerans. Generellt visade det sig att arter som förekommer långt norrut klarade sig bättre än de som kom växer sydligare när de hade härdats, och att höljearter klarade sig bättre än tuvarter.

I artikel två undersöktes hur vitmossans morfologi ändras i olika delar av en myr. Jag tittade på strukturer både hos enskilda skott och hos mossmattan. Från en myr samlades åtta arter, och jag fann att arterna kan delas in i två grupper som är starkt kopplade till förmågan att begränsa vattenförlusten som

sker genom avdunstning. Strukturen på mossmattans yta är hade stor betydelse. Tuvarterna hade slätare yta och mindre skott än höljararterna. Det var större variation i skottens och mossmattans egenskaper hos höljararter än hos tuvarter.

I tredje artikeln frågade jag var i Europa vitmossor är vanligast, och varför. Jag kom fram till att de flesta arter kan existera där skillnaden mellan nederbörden och avdunstningen ger ett tillräckligt fuktigt klimat, och denna klimatkombination ledde inte till mycket variation mellan arter. Störst påverkan på olika arters utbredning hade temperaturen, och framför allt dess variation över året. Störst variation är i regioner med kalla vintrar, vilket kan begränsa flera arters utbredning.

I den fjärde artikeln undersökte jag hur morfologin hos flytvitmossa (*Sphagnum cuspidatum*) och björnvitmossa (*S. lindbergii*) ändras över deras geografiska utbredningar. Flytvitmossa har en sydlig och björnvitmossa en nordlig utbredning i Sverige, men de överlappar varandra i norra Svealand och södra Norrland. Både dessa arter förekommer nära grundvattnet och konkurrerar potentiellt med varandra. Jag fann att den största skillnaden mellan arterna var att björnvitmossan bildade en slätare mossmatta. Hos bägge arterna vägde skotten översta del (där fotosyntesen äger rum) mindre ju längre man kommer från arternas utbredningscentra, och skillnaden mellan arterna var som minst i zonen där de finns tillsammans. Skillnaderna mellan arterna betingades troligen av en kombination av klimatets effekter på skottens tillväxt och på deras tolerans mot hårda vinterförhållanden.

Faktorer som sätter gränser för vitmossor är mer komplexa än man tidigare har trott. Vattentillgång är en faktor som begränsar i stort sett alla arters utbredning. Temperaturvariationen över året har olika effekt på olika arter, och påverkar både arternas utbredning i Europa och interaktionen mellan arterna inom myren.

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