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Catchment controls on mire properties in the post-glacial landscape

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Abstract

Mires are key ecosystems in the boreal biome which provide services related to carbon uptake, biodiversity, and regulation of hydrological and biogeochemical cycles. Minerogenic mires are supported by their upslope catchment area and underlying mineral soil, but a more detailed understanding and quantification of landscape drivers behind mire properties is needed. My thesis is focused on catchment controls on mire vegetation, and peat accumulation and expansion rates. The study was conducted in the Sävar Rising Coastline Mire Chronosequence in northern Sweden, where strong isostatic rebound has formed a natural age gradient that can be used for landscape level studies covering the Holocene. Given the similar climate, bedrock, and mineral soil properties across the area, the role of catchment eco-hydrological settings can be distinguished from that of mire ageing. Our results show that mire vegetation and recent nitrogen accumulation rates responded to catchment nutrient support, but older mires with deeper peat were also associated with lower plant productivity. In contrast, recent peat and carbon accumulation rates increased with mire age and a lower catchment supply of nutrients. The increase in peat and carbon accumulation rates with mire age was faster in hummocks than lawns, and after four thousand years hummock accumulation rates exceeded those in lawns. Mires in the area expanded non-linearly across the landscape depending on the availability of suitably wet areas. Mires occupied the wettest locations within one to two thousand years after land exposure and the slightly drier areas within three to four thousand years. Except for mires younger than a thousand years old, mire abundance was controlled by topography, while total mire area increase was a function of time and the formation of larger mire complexes. The results of this thesis contribute to the understanding of mire development at high latitudes and to scaling up our understanding of mire properties to the wider landscape level.

Keywords: chronosequence, catchment control, nutrient regime, MAR, CAR, NAR, peat accumulation, mire expansion, Holocene

Tillrinningsområdets inverkan på myrens egenskaper i det postglaciala landskapet

Abstrakt

Myrar utgör centrala delar av det boreala skogslandskapet. Till de ekosystemtjänster som myrar erbjuder hör upptag av atmosfäriskt kol, berikning av biodiversitet samt reglering av hydrologiska och biogeokemiska cykler. Minerogena myrar (kärr) erhåller vatten och näring från det uppströms liggande tillrinningsområdet eller från underliggande mineraljord. I min avhandling fokuserar jag på tillrinningsområdets betydelse för vegetation, torvackumulering och myrens förmåga att expandera. Studien utfördes nordost om Umeå, där den kraftiga landhöjningen har skapat en kronosekvens av myrar, som kan användas för studier på landskapsnivå över Holocen. Tack vare försumbara skillnader i klimat, berg- och jordart inom kronosekvensen kan tillrinningsområdets betydelse för myrens egenskaper särskiljas från myrens åldrande. Resultaten visade att vegetationen och graden av kväveackumulering gynnades av näring från tillrinningsområdet, samt att äldre myrar med djupare torvlager var mindre produktiva. Äldre myrar med lägre näringstillförsel ackumulerade torv och kol i snabbare takt jämfört med yngre myrar och ökningen med myrålder var snabbare i tuvor jämfört med höljor. Tuvornas ackumuleringsgrad av torv och kol överskred höljornas efter 4000 år. Den horisontella myrexpansionen bestämdes av tillgången till lämpligt fuktiga marker och var därför inte lineär över tid. Myrar koloniserade de fuktigaste områdena inom 1000–2000 år efter att landmassorna höjts ur havet, medan kolonisering av de något torrare områdena skedde inom perioden 3000–4000 år. Den totala myrarealen bestämdes av landskapets ålder och uppkomsten av myrkomplex, medan topografin avgjorde antalet myrar. Resultaten av den här avhandlingen bidrar till förståelsen för hur nordliga myrar utvecklas, samt till att skala upp myregenskaper till landskapsnivå.

Nyckelord: kronosekvens, tillrinningsområde, näring, MAR, CAR, NAR, Holocen, torvackumulering, myrexpansion

Flowering cloudberry (Swe. hjortron, *Rubus chamaemorus*)

Hummocks with flowering heather (Swe. ljung, *Calluna vulgaris*)

Förord

Då du strövar runt i den nordliga skogen händer det att du når en myr. Vid myrens rand stannar du till och försöker genast bilda dig en uppfattning om myrens karaktär: ”Kan jag korsa myren obehindrat eller behöver jag på förhand planera min rutt så att den kringgår de blötaste partierna? Kommer jag att hitta hjortron eller tranbär på just den här myren? Vilka fåglar trivs här?” Kanske påminner myren dig om din barndoms myr dit dina föräldrar tog dig på utflykt. Med ens väcks du ur dina tankar då några tranor lyfter från myrens bortre kant. En älgko med sin kalv har överraskat dem. Den fuktiga, solvarma mossan under dina fötter ger ifrån sig en härlig doft av myllrande liv. Hur härlig myren är under sensommaren! Här vill jag stanna en stund.

Myrar har förbryllat och fascinerat, livnärt och oroat människan genom århundraden. Med modern teknik och forskning kan vi mer ingående än tidigare förstå hur myrar samverkar med och påverkas av sin omgivning, framförallt sitt tillrinningsområde. Genom den kunskapen kan vi bevara de myregenskaper som är så viktiga för biologisk mångfald, kolinlagring och reglering av vattenflöden genom landskapet - och inte minst den otroliga naturupplevelse som myrar erbjuder. I den här andan hoppas jag att min avhandling kan bidra med värdefull information och ny kunskap till alla myrentusiaster och övriga naturvänner där ute. För mig återstår nu enbart att tillönska er en trevlig läsning!

Betty Ehnvall
Bygdeå, september 2023

Flowering cotton deergrass (Swe. snip, *Trichophorum alpinum*)

Dedication

For Peter, Ivar and Ebba

‘A human lifetime is so short that we usually do not appreciate changes occurring in the landscape.’

Tore Påsse and Johan Daniels 2015

Micro-topography ranging from hollow forming wet flarks to hummock forming dry strings

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

Ehnvall, B.*, Ågren, A.M., Nilsson, M.B., Ratcliffe, J.L., Noumonvi, K.D., Peichl, M., Lidberg, W., Giesler, R., Mörth, C.M., Öquist, M.G. (2023). Catchment characteristics control boreal mire nutrient regime and vegetation patterns over ~5000 years of landscape development. *Science of the Total Environment*, 165132.

Ehnvall, B.*, Ratcliffe, J.L., Olid, C., Smeds, J., Bishop, K., Klaminder, J., Li, C., Nilsson, M.B., Öquist, M.G. Topographical and hydrogeochemical controls on recent carbon and nitrogen accumulation rates in a post-glacial mire chronosequence (manuscript).

Ehnvall, B.*, Ratcliffe, J.L., Bohlin, E., Nilsson, M.B., Öquist, M.G., Sponseller, R.A., Grabs, T. (2023). Landscape constraints on mire lateral expansion. *Quaternary Science Reviews*, *302*, 107961.

Ehnvall, B.*, Ratcliffe, J.L., Nilsson, M.B., Öquist, M.G., Sponseller, R.A., Grabs, T. Topography and time shape mire morphometry and large-scale mire distribution patterns in the high-latitude landscape (submitted manuscript).

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* Corresponding author

Seeds of pod grass (Swe. kallgräs, *Scheuchzeria palustris*)

Abbreviations

BBL	Bothnian Bay Lowlands
BD	Bulk Density
BP	Before Present
CAR	Carbon Accumulation Rate
DEM	Digital Elevation Model
DM	Dry Matter Content
GEE	Google Earth Engine
GIS	Geographical Information Systems
LOI	Loss on Ignition
MAR	Mass Accumulation Rate
NAR	Nitrogen Accumulation Rate
NDVI	Normalised Difference Vegetation Index
NPP	Net Primary Productivity
PGR	Peat Height Growth Rate
SMC	Sävar Rising Coastline Mire Chronosequence
SMI	Soil Moisture Index

Bogbean (Swe. vattenklöver, *Menyanthes trifoliata*), bottle sedge (Swe. flaskstarr, *Carex rostrata*), white water lily (Swe. vit näckros, *Nymphaea alba*) and bog-myrtle (Swe. pors, *Myrica gale*) in mire pond

1. Introduction

High-latitude mires provide many important ecosystem services from mediation of hydrological and biogeochemical cycles, within, up- and downstream of the mire area (Fergus et al., 2017; Helbig et al., 2020a, 2020b; Lane et al., 2018; Sponseller et al., 2018), to flood attenuation, primarily by reducing peak flow (Waddington et al., 2015), and regulation of water quality through the export of water and nutrients downstream. In addition to influencing the lateral flow of energy and matter across the landscape, mire ecosystems store considerable amounts of carbon as a result of carbon uptake from the atmosphere, resulting in long-term peat accumulation (Loisel et al., 2014). Finally, mires are important habitats that support biodiversity (Joosten, 2003). To quantify and scale-up the various functions and ecosystem services provided by high-latitude mires, it is important to consider where and when they have formed, how they have developed, and how they are shaped by spatiotemporal drivers. A conceptual understanding of drivers of the extent and properties of mires is fairly well developed (e.g. Ivanov, 1981). However, few studies have attempted to quantify these drivers, especially at larger spatial scales. My thesis aims to fill this knowledge gap by contributing to the understanding of how the landscape surrounding mires controls their spatial extent and inherent properties.

1.1 Mires in the hydrological boreal landscape

Mires are characteristic of the boreal landscape mosaic, along with forests and lakes (Figure 1). The persistence of these three landforms ultimately depends on local hydrological conditions (Ivanov, 1981). Theoretically, mires are found in landscape positions where flow paths accumulate water and saturate the soil surface while, in contrast, drier upland areas are mainly covered by forests and water-filled basins occupied by lakes. The two main controls on local flow paths are climate (Treat et al., 2019) and topography (Graniero and Price, 1999). Importantly, however, mires can modify local hydrological conditions to suit the mire vegetation (van Breemen, 1995), which makes the boundary between different landscape elements diffuse rather than defined by distinct sets of environmental conditions (Ohlson et al., 2001; Ratcliffe et al., 2017; Velde et al., 2021). This observation suggests that it is worth studying the interface between the areas around mires and the wider upland area, as this may reveal controls on the lateral extent of mires and their opportunities to expand further upland.

Minerogenic mires (fens) interact with the surrounding, hydrologically connected, upland area as well as other surface water bodies (Lane et al., 2018). This type of mire ecosystem mainly receives water and nutrients from the upslope catchment area or from groundwater intrusions from below (Ivanov, 1981; Romanov, 1968). Having passed through a minerogenic mire, water may then be discharged from one or several outlets (Sirin et al., 1998), diffused over wider outlet zones (Sallinen et al., 2019), or lost to aquifers through deep seepage (Hokanson et al., 2020; Marttila et al., 2021). Particulate or dissolved elements may also be transported downslope from the mire area by discharge water, depending on the mire's nutrient and water regimes (Fergus et al., 2017; Sponseller et al., 2018). Consequently, minerogenic mires can mediate fluxes of water and/or nutrients across the landscape. In this thesis, 'nutrient regime' and 'water regime' refers to the inflow, accumulation, and transformation of nutrients and water over the mire area (Zhao et al., 2013).

In contrast to minerogenic mires that are hydrologically well-connected to the surrounding landscape, ombrogenic mires (bogs) receive water exclusively from precipitation (Sjörs and Gunnarsson, 2002). Consequently, ombrogenic mires are hydrologically more isolated from the surrounding landscape than are minerogenic mires.

Hydrologically the division between minerogenic and ombrogenic mires is strict, yet, depending on the external nutrient supply (Avetov et al., 2021) and internal nutrient cycling within the mire area (Jonasson and Shaver, 1999), minerogenic mires can represent a wide spectrum of nutrient regimes ranging from eutrophic to oligotrophic. As a result, plant species compositions in nutrient-poor minerogenic mires may resemble those of ombrogenic mires (Laine et al., 2021a). Similarly, mire vegetation is not defined by specific plant phyla or functional groups, but ranges from aquatic or semi-aquatic plant species (Granath et al., 2010; Gunnarsson, 2005) to purely terrestrial plant species (Moor et al., 2017). In this thesis the focus is on minerogenic mires, from now on referred to as 'mires' if no other description is given, which represent the majority of peatlands in our geographical area of interest and at high latitudes in general (Figure 3).

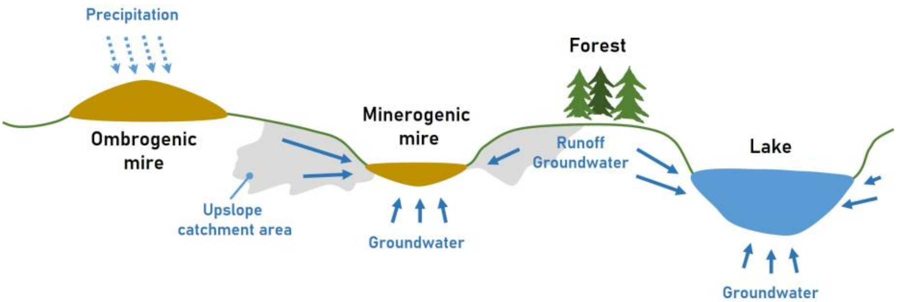

Figure 1. The boreal hydrological landscape and its key components; mires, lakes, and forests connected through flow paths. Ombrogenic mires receive water exclusively from precipitation, while minerogenic mires, lakes, and upland forests may be connected via surface runoff or surficial groundwater flow paths. In addition to the upslope catchment area, minerogenic mires and lakes may be supported hydrologically from deep groundwater intrusions.

1.2 Mire initiation and peat lateral expansion

A positive seasonal water balance is the main requirement for mire initiation and persistence, since saturated soil will result in anoxic conditions and ensure that mire net primary productivity (NPP) rates exceed decomposition rates, allowing for peat to accumulate (Ivanov, 1981). Mires can be initiated in one of three different ways, which in this thesis are referred to as 'primary mire formation', 'terrestrialisation' and 'paludification'. Regardless of initiation type, the establishment of peat forming plant communities is a prerequisite for mire initiation (Rydin and Jeglum, 2013).

Primary mire formation, or xerarch succession, takes place in land areas not occupied by any other (terrestrial) vegetation types. Mires that initiate through primary mire formation thus form directly on wet mineral soil (Rydin and Jeglum, 2013). The most extensive areas of primary mire formation today can be found in post-glacial landscapes that were covered by a thick ice sheet during the last glaciation and where new land areas became exposed above sea level during the Holocene due to isostatic rebound. Examples of such regions are the Bothnian Bay Lowlands in Fennoscandia (Ehnvall et al., 2023; Laine et al., 2021a), the Hudson and James Bay Lowlands in Canada (Pendea and Chmura, 2022), the shores along the White Sea in Russia and Antarctica (Wright et al., 2008).

If vegetation by pond, lake, or bay shores becomes peat accumulating, mires can initiate in these locations through terrestrialisation, also referred to as hydrarch succession (Rydin and Jeglum, 2013). Terrestrialisation may be further supplemented by the accumulation of sediments at the basin bottom. A lake may become completely filled up with peat and sediments, but a stable open water body can also remain if the lateral expansion of peat outranges terrestrialisation (Johnson and Miyanishi, 2008).

Finally, the term paludification is used both to describe a specific mire initiation process and to describe any lateral expansion of peat. Paludification as a mire initiation type describes peat formation at sites previously occupied by terrestrial vegetation, in our case boreal forest (Vitt, 2013). When soil becomes wetter, typical mire plant species may be favoured over ‘upland species’ adapted to drier conditions. Shifts in the local hydrological regime may be caused by changes in climate or in land-use/land-cover. For example, vegetation removal through forest fires or clearcutting can reduce evapotranspiration and water uptake by plants, which results in wetter surface soil that may generate suitable conditions for mire initiation (Schaffhauser et al., 2017). Beaver dams may also cause paludification locally and regionally (Nummi et al., 2018).

Once a mire has formed, through any of the three initiation types, continued peat accumulation may lead to vertical and/or lateral peat expansion given favourable hydrological conditions. At the interface between mires and forests, paludification can proceed over time, and even be supported by the mire area under less favourable topographic or climatic conditions (van Breemen, 1995). In this way, established mires may expand to areas that were originally insufficiently wet for mire initiation (Kulczyński, 1949; Ruppel et al., 2013).

1.3 Land uplift-based mire chronosequence studies

Mire initiation and expansion rates (both vertical and lateral) are often studied using peat chronologies (Quik et al., 2022) or bottom sediment analyses (Huikari, 1956). While being highly accurate at the level of the individual mire or sampling point, these techniques are often costly, time-consuming and not applicable at larger spatial scales. Mire chronosequences, which trade space for time, provide a useful alternative to peat chronologies for studying mire processes spanning long time scales at the landscape level (Johnson and Miyanishi, 2008).

Space-for-time substitutions require that a site offers a gradient which encompasses relatively large age differences within a limited geographical area (Figure 2). Such gradients can be found, for instance, in coastal areas with strong isostatic relaxation, where ecosystem age is a direct function of elevation above sea level. Mires found close to the present coastline are young, while mire age increases with altitude and distance from the present coastline, up to the highest historical coastline (Tuittila et al., 2013). Above the highest coastline, mires will not be part of the chronosequences, since at this point land surface age does not increase with increased altitude. The land uplift-based mire chronosequence approach relies on the assumption that mires in coastal areas initiate soon after land exposure from the sea and, consequently, mire ages cannot exceed the maximum age of the mineral soil surface. Examples of mire chronosequences that have frequently been used for scientific research are the Sävar Rising Coastline Mire Chronosequence (SMC) used in this thesis and the Nyby chronosequence (Laitinen et al., 2016) along the shores of the Bothnian Bay Lowlands (BBL), and chronosequences in the James and Hudson Bay Lowlands (Martini and Glooschenko, 1985).

In parallel with the development of ecosystems, land uplift based chronosequence models can also be used to describe the aging of mineral soils. Once mineral soil has been exposed from the sea, it becomes prone to weathering. Easily weatherable minerals, such as phosphorus-releasing apatite, may disappear from the surface soil within only five hundred years (Giesler, 2010), while it takes up to 2 000 years for the potassium- and calcium-releasing biotite and hornblende to be completely removed from the topsoil through weathering (Hoffland et al., 2002). Consequently, depending on a mire’s position along the chronosequence, it should receive different amounts of mineral nutrients from corresponding upland areas based on the gradient of weathering derived nutrients (Starr and Lindroos, 2006). The decrease in mineral nutrient transport to mires in older parts of the landscape is here referred to as ‘oligotrophication’. In contrast to ‘ombrotrophication’ (i.e. the succession from minerogenic to ombrogenic conditions), which is unlikely in the high-latitude landscape, ‘oligotrophication’ is likely to cause nutrient depletion in the high-latitude landscape.

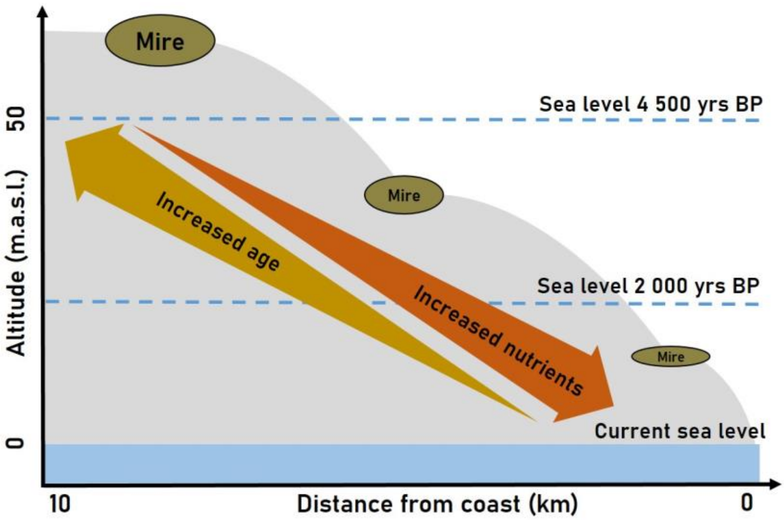

Figure 2. Conceptual overview of the land uplift-based mire chronosequence approach. The maximum age of mires in different parts of the chronosequence cannot exceed the land surface age. Mires found close to the present coastline are generally younger and smaller, compared to older mires further inland that have expanded laterally to cover larger areas. Mires in younger parts of the chronosequence are more nutrient-rich due to 1) shallower peat depths and closer distance to underlying mineral soil and 2) more mineral nutrients remaining in un-weathered upland catchment areas.

1.4 Knowledge gaps and thesis objectives

Although mire hydrology and biogeochemistry has been studied over the past hundred years or more (e.g. Gorham, 1957; Kulczyński, 1949; Malmström, 1923; Sjörs, 1950), and the conceptual understanding of drivers behind the properties of minerogenic and ombrogenic mires was formulated long ago (Heinselman, 1970; Ivanov, 1981), few studies have attempted to quantify these drivers. Most efforts to describe the hydrological drivers behind mire development have focused on ombrogenic systems and the development of raised bogs (Clymo, 1984), while studies focusing on minerogenic mires remain under-represented in the scientific literature. Specifically, there are few studies which describe different sets of ecohydrological characteristics in catchments and their control over mire properties such as mire nutrient regime and NPP, as well as mire functions including carbon accumulation and mire lateral expansion patterns. This has historically limited our understanding of how the catchment supports high-latitude mires. The overall aim of this thesis is to fill that knowledge gap, by describing long-term mire-landscape interactions in the high-latitude landscape. Specifically, the objective is to scale-up measured mire properties from the level of an individual mire or sampling point to the landscape level using remotely sensed data, and to quantify landscape controls on minerogenic mire extent, properties, and patterns at large spatial scales. This thesis is based on four studies referred to as papers I-IV. The background and specific objectives of each paper are:

- Paper I: Mire vegetation holds the key to characteristic mire properties including surface micro-topography (Eppinga et al., 2010; Glaser et al., 1990) and biodiversity (Joosten, 2003). Despite a long history of botanical studies, drivers behind mire vegetation patterns have previously been poorly addressed at spatial scales exceeding the individual mire level. The objective of paper I was to assess catchment controls on mire nutrient regime and vegetation patterns over the past 5 000 years, and to scale up catchment controls to the landscape level using terrain indices. Specific objectives were to test (i) whether the normalised difference vegetation index (NDVI) reflects variation in surface peat nutrient concentrations, (ii) whether variation in mire NDVI can be described based on ecohydrological catchment characteristics, and (iii) whether mire NDVI is controlled by Holocene landscape age.

- Paper II: High-latitude mires represent a considerable part of the global soil carbon pool, holding ~ 80 % of the global peatland carbon stock (Hugelius et al., 2020; Loisel et al., 2014). While contemporary peat, carbon, and nitrogen accumulation rates define a mire's scope to function as a long-term carbon and nitrogen store, spatiotemporal controls on these accumulation rates have been poorly described at larger spatial scales and over time. The objective of paper II was to study recent peat, carbon, and nitrogen accumulation rates in mires spanning a 5 000-year age gradient. Specific objectives were to study (i) how recent peat, carbon, and nitrogen accumulation rates have changed over 8 000 years of mire development, (ii) how accumulation rates vary in response to catchment hydrogeochemistry and nutrient availability, and (iii) how peat, carbon, and nitrogen accumulation rates and their responses to spatiotemporal drivers differ between micro-topographical features at the mire surface.

- Paper III: Lateral expansion of mires is widely considered to be a non-linear process controlled by the surrounding topography, which results in different lateral expansion rates of peat over the course of mire development (Loisel et al., 2014; Payne et al., 2016; Ruppel et al., 2013). Despite observations from individual mires confirming the non-linearity of mire expansion (Ruppel et al., 2013; Weckström et al., 2010), constant expansion rates are still often applied when peat accumulation rates are calculated from basal dates (Nichols and Peteet, 2019; Yu et al., 2010). The objective of paper III was to estimate mire lateral expansion rates in the coastal areas of northern Sweden over the past 9 000 years. The hypotheses were (i) that mire areal increases have been non-linear, and (ii) that they are associated with land areas available for mire growth and expansion, which in turn are related to topo-edaphic controls.

- Paper IV: Individual mires are part of the characteristic boreal landscape mosaic. Despite their importance for various functions at the ecosystem and landscape levels, and ecosystem services, the spatiotemporal arrangement and drivers behind mire patterns have rarely been studied at larger spatial scales. The objective of paper IV was to quantify the relationship between mire morphometry and upland hydrotopography over 9 000 years of landscape development. Specific objectives were to study (i) whether mire coverage and abundance increase with time, (ii) whether peat lateral expansion has resulted in larger, more complex mire shapes in older parts of the landscape, in contrast to smaller mires with simpler shapes in younger parts of the landscape, (iii) whether catchment settings control mire lateral expansion, and (iv) whether landscape slope and wetness can explain mire morphometry.

Colour shifts in *Sphagnum* species across the micro-topographic gradient in an old chronosequence mire

2. Methods

2.1 Study approach

My co-authors and I, from now on referred to as 'we', used the Sävar Rising Coastline Mire Chronosequence (SMC; Figure 3) in the northeast of Sweden to describe mire-landscape interactions over the Holocene time-scale. The thesis covers mire-landscape interactions at spatial scales ranging from the individual sampling point level at mires visited in the field (papers I-II), through the whole-mire and catchment levels (papers I-II and IV), to all mires within landscape-age classes spanning 1 000 years each (papers III-IV). To test the hypotheses and research questions outlined for each of the papers, we applied the following study approaches:

- Paper I: Catchment controls on mire vegetation patterns were studied at the sampling point, whole-mire, and landscape levels (including mires in the extended chronosequence area). Mire vegetation patterns were described using the normalised difference vegetation index (NDVI), while the mire nutrient regime was described using the surface peat elemental composition, and catchment characteristics were extracted based on different digital map sources. The elemental concentrations in peat and catchment characteristics were used as predictive variables in monthly OPLS models to identify drivers behind mire NDVI patterns. We distinguished between open and tree-covered mires in the models.

- Paper II: Recent (<100 year) peat, carbon, and nitrogen accumulation rates were estimated for nine mires based on peat cores representing two micro-topographical features (hummocks and lawns). Peat chronologies were established using ^{210}Pb and spheroidal carbonaceous particles (SCP) techniques. Drivers behind accumulation rates were identified using OPLS models separately for hummocks and lawns, with predictive variables represented by mire age and peat depth, water table level, nutrient regime, sampling point NDVI, and catchment characteristics.

- Paper III: Mire utilisation of hydrologically suitable areas was calculated over 1 000-year age zones across ten mire chronosequences (of which the SMC was one) covering a total of 5 500 km^2 along the rising coastline of northern Sweden. To identify areas hydrologically suitable for mires, we applied two thresholds to the Swedish soil moisture index (Ågren et al., 2021) based on the present moisture of mires within the chronosequences. Cumulative mire areas over the age-classes were normalised to hydrologically suitable areas, to demonstrate that topo-edaphic controls on mire areal extent results in non-linear expansion patterns over time.

- Paper IV: We described mire morphometry over 1 000-year age-zones in the SMC using simple area and shape indices. Slope and moisture conditions in mire-surrounding areas were used to examine upland hydro-topographical controls on mire morphology, with the upland areas being examined at increasing spatial scales, from all mire surrounding areas within 20 m from the mire to the entire upslope catchment area and, finally, all non-mire areas within each 1 000-year age zone. We used the catchment-to-mire ratio to describe the hydrological support to the mires in the chronosequence.

2.2 Selection of study objects

For this thesis, we extended the SMC from previously studied mires to include all mires in the area from the present coastline to the 9 000-year coastline, reaching around 30 km inland (63° 40'- 64° 10' N, 20°20'- 20°50' E) and covering a total area of around 550 km^2 (Figure 3). For spatial analyses at the mire and landscape levels, we used mires defined in the Swedish property map provided by the Swedish Mapping, Cadastral, and Land Registration Authority (Lantmäteriet, 2020). Each of the studies included in my thesis covers different parts of the chronosequence area:

- For paper I, we needed to include pristine mires for surface peat sampling, to exclude the impacts of mire drainage on peat elemental and plant species compositions. To achieve this, we selected 47 mire objects in the 0-5 000 age range for sampling. We excluded the most heavily drained mires from the mire population before scaling up mire properties from the sampled mires to the landscape level, resulting in 1 576 mire objects in the 0-5 000 year age-range which could be used for landscape level analyses.

- In paper II we made use of already-extracted peat cores from six intensively studied chronosequence mires (Laine et al., 2021a; Wang et al., 2023), but complemented these with cores from two older mires to expand the sample to represent a landscape age of around 4 500 years. Chronosequence mire sampling points were located at 1.5-53.6 meters above sea level (m.a.s.l.). We also included an old reference mire close to the highest coastline, the intensively studied Degerö Stormyr (Noumonvi et al., 2023).

- Paper III covers all mires described in the Swedish property map in the 0-9 000 year age-range. While papers I-II and IV are based on the SMC, paper III also covers nine additional chronosequences along the rising coastline of the Swedish Bothnian Bay Lowlands (BBL), and thus compares the SMC to the regional context.

- In paper IV we used mires in the 0-9 000 year age-range, but excluded mires smaller than 2 500 m^2, as these have been only sporadically mapped. Inclusion of the smallest mires would have risked bias towards areas with more comprehensive mapping of small mire objects, which could have altered the descriptions of mire patch distributions in the SMC. Paper IV covers a total of 3 056 mire objects.

To illustrate the main selection of mires and the variation in vegetation and surface peat properties therein, we prepared an interactive map of the mire chronosequence area, which can be used as a basis for selecting mire objects to include in future studies in the SMC area. The interactive map can be found using the web address: https://slughg.github.io/MiresChrono.

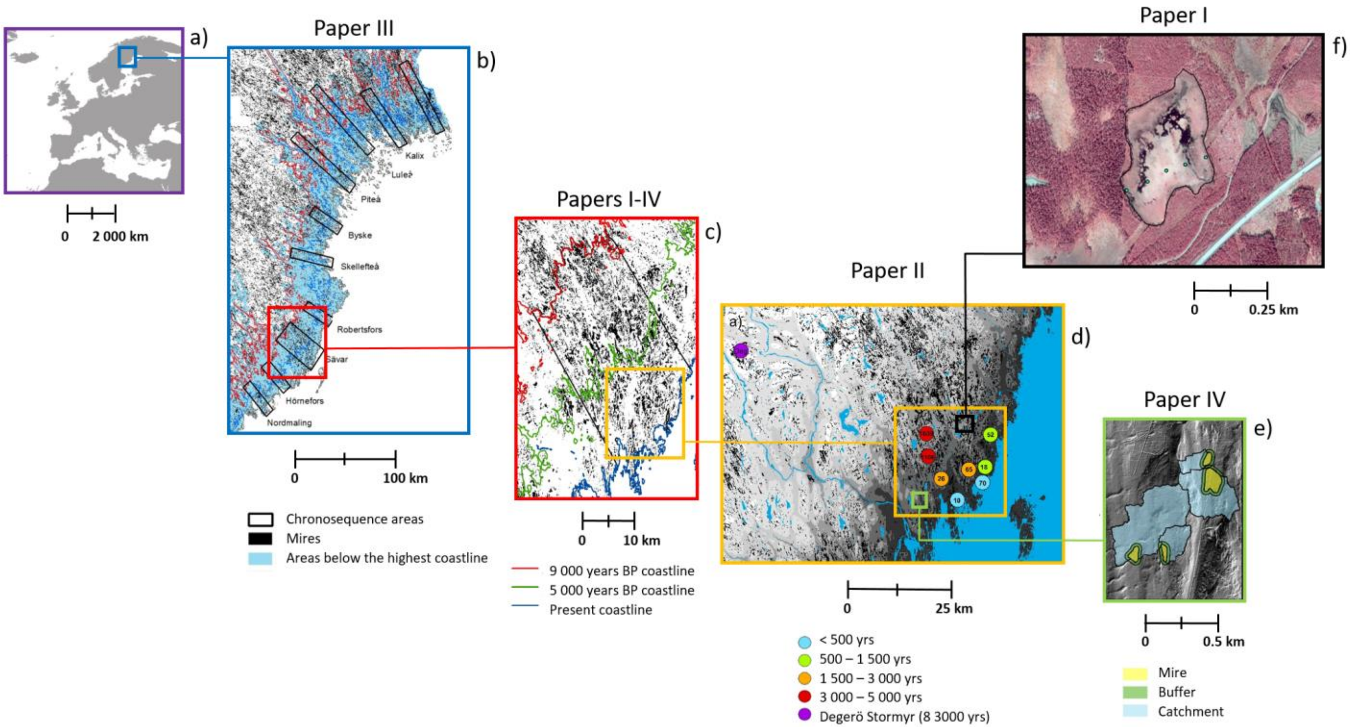

Figure 3. Spatial arrangement of study objects covered by papers I-IV a) at the national level, b) in the Bothnian Bay Lowlands (BBL; paper III), c) in the Sävar Rising Coastline Mire Chronosequence (SMC; papers I-IV), d) in selected, heavily studied chronosequence mires (paper II), e) at the catchment (paper I-II and IV) and mire buffer levels (paper IV), and f) in edge-to-edge sampling transects (paper I).

2.3 Climate and geology in the chronosequence area

The SMC is found in the boreal biome, and is shaped by a sub-arctic climate. Over the 1991-2020 reference period, annual temperature averages were 3.5ºC (July: 15.7ºC; January: -6ºC) and average annual rainfall was 654 mm (July: 79 mm; January: 48 mm; Swedish Meteorological and Hydrological Institute). The SMC is dominated by minerogenic mires and lies in the southern mixed mires region, also referred to as the aapa mire sub-region (Gunnarsson et al., 2014). Mixed mires are characterised by various patterns of micro-topographical features such as hummocks, lawns, hollows and ponds, listed from the driest to the wettest micro-topographical form. If micro-topographical forms are arranged in larger patterns, mires can be classified as string mires, net mires, or other formations, based on the arrangement of hummock-forming strings and hollow-forming flarks (Rydin et al., 1999). Within the SMC, string mires are particularly common in the older parts of the landscape, while younger mires may have rather homogenous surfaces without prominent micro-topography. Mixed mires may also contain larger sub-sections with distinct vegetation types resulting from different nutrient and hydrological regimes in different parts of the mire (Sallinen et al., 2023).

The bedrock of the SMC is dominated by paragneiss, predominately made of quartz, mica, and feldspar, but mafic (basaltic andesite, gabbrodiorite) and felsic (granodiorite, granite) rock intrusions are also present, according to bedrock maps (1: 50 000) by the Geological Survey of Sweden. Landforms typical of the SMC cover elongated wave-exposed ridges of glacial till (drumlins) interlaid by valleys of deposited postglacial clay, silt, and sand (Lindén et al., 2006). Of these, the depressions are best suited to mires, both because the lower terrain positions result in the greater accumulation of water flow paths necessary to sustain wet soil conditions, and because the finer sediments in the depressions have lower permeability, which is likely to further promote saturation of the surface soil. In addition to the elongated, topographic features across the SMC, a small river (Sävar) traverses the chronosequence. Floodplains along river Sävar, with lacustrine and glacio-lacustrine sediments, are highly suitable for mire initiation and development since these areas are continuously rewetted by the river as the water level fluctuates. However, for the same reason, floodplain mires in the area differ from the remaining chronosequence mires in terms of flow direction and genesis (Lane et al., 2018). Hence, we excluded floodplain mires along river

Sävar from the studies considered in this thesis, as these mires do not follow the typical mire development predicted by the mire chronosequence. Based on their shapes and positions along the river Sävar, four mires with a total mire area of 3.6 km^2 were identified as floodplain mires, and removed from the mire map.

2.4 Estimating age from shore displacement curves

The chronosequence approach in the SMC relies on estimations of land surface age (T_{age}) from the elevation above sea level (z). To achieve such estimates, shore displacement curves are often combined with elevation data, gathered from field measurements or, as in the case of this thesis, rendered from digital elevation models (DEM). Shore displacement curves can be generated using various post-glacial landscape features present in the study area which mark the uplift of the seashore. One of the most common approaches to estimate land-uplift in Sweden is the use of laminated, or varved, lake sediments from lakes at different elevations (Renberg and Segerström, 1981). The annual sedimentation cycle in a lake is characterised by the deposition of three or four varves of different colours depending on the origin of the deposited sediment (autochthonous or allochthonous). Each varve in the sediment thus represents an annual cycle of sediment accumulation (Zillén, 2003). For the work presented in this thesis, we applied two different shore displacement curves for the SMC. For papers I-II and IV we used a local shore displacement curve (Eq.1), based on varved sediment from six lakes in the area (Renberg and Segerström, 1981).

Eq. 1 $$T_{age} = -0.287z^2 + 99.967z$$

In paper III, shore displacement models provided by the Geological Survey of Sweden were applied (Eq.2 for the SMC; Påsse and Daniels, 2015). The model was developed for the whole of Sweden based on empirical data covering lake tilting, tide gauge, and markers of the highest coastline, as well as shore-level curves (Påsse and Daniels, 2015). As paper III covers not just the SMC but nine additional chronosequences in the Swedish BBL area, it was desirable to apply shore displacement curves based on similar modelling approaches for all the included chronosequences.

Eq. 2 $$T_{age} = -0.1818z^2 + 82.713z + 421.07$$

The two shore displacement curves generate similar land surface ages for young parts of the SMC, below 8 000 years BP, while differences in estimated land surface age increase in the oldest parts of the chronosequence exposed during the early Holocene. In the oldest parts of the SMC, the lake sediment-based shore displacement curve (Eq. 1) predicts slightly lower ages from the elevation above sea level than the regional shore displacement curve does (Figure 4). It is worthwhile mentioning though, that the local lake sediment-based shore displacement curve (Eq.1) was generated based on lakes in the 29-177 m.a.s.l. range and is thus less applicable to extrapolations above these elevations. For the results presented in this thesis, the differences in ages resulting from the use of the two curves is negligible in papers I and II, since these cover chronosequence mires in the 0-5 000 year BP range for which the curves predict very similar land surface ages. For papers III and IV, differences in land surface age predicted by the curves mainly affect the interpretation of mire patterns in the oldest part of the chronosequence.

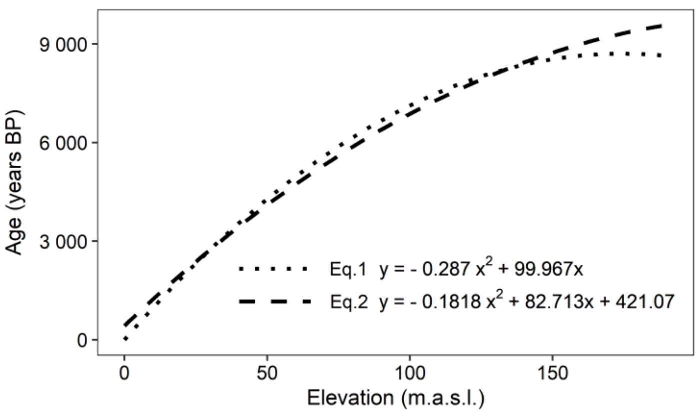

Figure 4. Mire shore displacement curves applied in papers I-II and IV (Eq. 1; dotted line), and paper III (Eq.2; dashed line) generate similar land surface ages for the young and intermediate parts of the chronosequence (younger than 8 000 years BP, at elevations below 150 m.a.s.l.,), with increased differences in estimated ages emerging above approximately 8 000 years BP).

It is important to note that the establishment of mires can lag behind land exposure considerably if the climate was historically drier (Morris et al., 2018), substrate conditions were initially unsuitable (Gorham et al., 2007), or plant dispersal rates or NPP were slow (Sundberg et al., 2006; Tiselius et al., 2019). Based on the potential lag in mire initiation, whenever possible we have used elevation-based ages in this thesis to describe the land surface age in mire-surrounding upland areas (papers I and IV), rather than to describe the actual mire age. Where elevation-based ages have been used to describe land surface age in mire-surrounding upland areas, we have indicated a mire's position along the chronosequence using its elevation (papers I and IV) and distance to the present coastline (paper I). With this precaution, we can confidently apply ages estimated from the shore displacement rate.

2.5 Generation of peat data

2.5.1 Fieldwork and sampling

For this thesis, I visited 71 chronosequence mires in the SMC, covering 94 sampling transects comprising a total of 470 sampling points. Fieldwork took place during July-August 2018 (sampling for paper I) and July 2020 (peat coring at two of the mires included in paper II). In addition, paper II covers peat cores collected by colleagues from seven mires visited during July-August 2019 (Smeds et al., 2022), as well as automatic and manual water table level measurements from June-August 2022-2023 (Engman, 2022). In our interactive mire map, we show all mires that were sampled as a part of this thesis: https://slughg.github.io/MiresChrono.

Mires sampled for paper I were selected based on three criteria: 1) they should not be affected by visual (from map inspection) ditches within 50 m of the sampling point, 2) they had to be evenly distributed across the 5 000 year age gradient, and 3) they should represent different sizes. At a majority of the selected mires, sampling transects with five edge-to-edge sampling points per mire transect were applied (Figure 3f), with the outermost points being placed 10 m from the mire edge. On the smallest mires, the edge points were placed 5 m from the mire edge due to the short distance across the mire surface. The mire edge was defined on site based on vegetation and peat depth (> 30 cm peat), and the intermediate and central sampling point positions were adjusted based on the fixed position of the edge points. All sampling transects were located perpendicular to the direction of the isostatic rebound, to minimise large-scale slope effects and possible age gradients that could influence the larger mire complexes in older parts of the chronosequence in particular. Sampling points were mapped using a Trimble GeoExplorer 6000 GPS with a vertical and horizontal precision of 0.02 m (Trimble Navigation Limited, 2012).

At each sampling point, a 10 cm deep surface peat sample (6 x 6 cm) was collected for analysing peat bulk density, dry matter content, and organic matter content, as well as elemental concentrations in the peat (Figure 5e). The interphase between the living vegetation consisting of *Sphagnum* moss or vascular plants, depending on the mire, and the peat surface was identified based on the structure of the substrate. The living part of the plants was removed and a peat sample collected from the underlying bulk peat. A separate peat sample was collected from the same depth to measure electrical conductivity and pH. The peat samples were stored in plastic bags and placed in a freezer (-18°C) within 8 hours of extraction. Peat depth was measured manually by pushing a metal rod through the peat until it reached a non-penetrating surface representing the vertical distance from the mire surface to underlying bedrock, rock, or mineral sediment. The horizontal distance to mineral soil at each sampling point was later mapped from the sampling point position to the nearest point along the edge of the mire polygon. For the final chemical analysis in paper I, not all of the sampled mires could be included, so a second mire selection following the initial selection criteria was carried out. Paper I eventually covered surface peat samples from 47 mires.

Paper II included extraction of 50 cm deep cores from eight chronosequence mires and from the older Degerö Stormyr (Noumonvi et al., 2023). Peat cores were collected using a cylindrical peat corer with an inner diameter of 15.1 cm (modified from Clymo, 1988). All cores included the living vegetation and were sampled using the mire surface as the reference level. Two cores were collected from the mires: one representing a hummock and one representing a lawn (Figures 5a-b). In one of the youngest mires (S10) hummocks were absent and, consequently, a single core represented the micro-topographically homogenous mire lawn surface, generating a total of 15 peat cores. In another of the youngest mires, peat depth was shallower than 50 cm, and cores of just 30 cm (lawn) and 26 cm (hummock) could be collected. Peat cores were stored in water and air-tight PVC plastic tubes sealed with plastic caps and transported to a freezer (-18°C) within 6 hours of extraction. The peat cores were cut into 2 cm thick discs (25 per core for 50 cm cores) within a month of extraction. The cutting was performed at temperatures of less than 4°C, to generate undisturbed discs, using a band saw with a stainless steel blade. The discs were weighed for wet bulk density measurements and stored in airtight plastic bags, then returned to the freezer immediately (-18°C) after cutting.

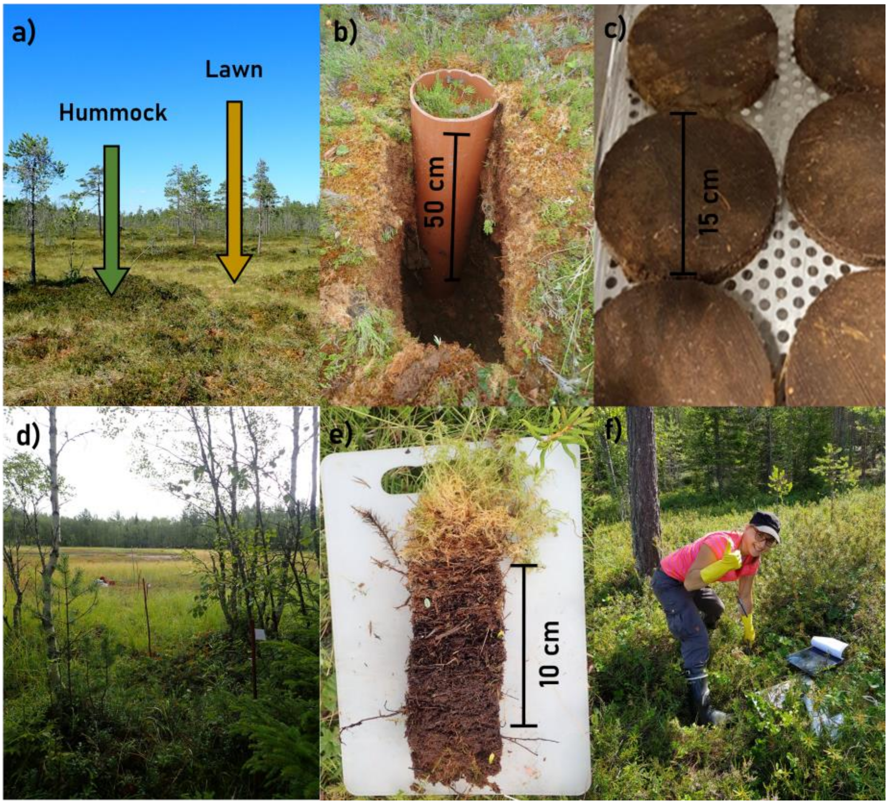

Figure 5. Peat core sampling in July 2020 for paper II (a-c) and surface peat sampling for paper I (d-f) in July-August 2018. 50 cm deep peat cores were collected from hummocks and lawns (a) using PVC tubes (b) and a cylindrical peat corer. 10 cm surface peat samples (e) were collected from five sampling transects crossing the mire surface, where the edge points were located 10 m (or in the smallest mires 5 m) from the mire edge. In d) sticks mark two-meter intervals between the mire edge and the edge-sampling point. Peat cores were cut to 2 cm thick discs before further analysis (c). Photos by Betty Ehnvall (a-b, d-e), Jacob Smeds (c) and Clydecia Spitzer (f).

2.5.2 Peat processing and chemical analyses

Surface peat samples for paper I were oven dried (at 60ºC for 72 h) and cooled in desiccator to avoid moisture adsorption before being homogenised and ground for 1-3 min, depending on the substratum, at a rotating speed of 25 000 rpm (IKA Tube Mill Control, version 1.4). Large roots (diameter of over 1 mm) were removed before grinding. Peat samples used for paper II were treated in a similar fashion, but four of the cores were freeze-dried rather than oven-dried prior to grinding (Smeds et al., 2022). Organic matter content (OM %) was measured for all peat samples (papers I-II) after drying samples overnight at 105ºC (generating the dry mass), followed by loss on ignition (LOI) for 6 h at 550ºC. Peat conductivity (INESA DDS-307) and pH (Greisinger GMH5530) were measured at 20ºC from peat slurries (paper I) prepared from melted peat samples. 50 ml milli-Q water was added to equivalent to 2 g dry peat, shaken for 15 minutes and left overnight before measurements were taken.

Elemental concentrations used in paper I were analysed using Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES), Inductively Coupled Plasma Mass Spectrometry (ICP-SFMS) and, in the case of nitrogen and carbon, using an Elemental analyser (Flash EA 2000, Thermo Fisher Scientific). All of these are described in the paper. Samples analysed using ICP-SFMS represented pairs of edge-centre transect points from 33 mires (n = 66), while samples analysed using ICP-OES represented entire sampling transects with five points each from 14 mires (n = 70). Elemental concentrations were expressed on the basis of dry matter content, from which analytical background concentrations were excluded.

Variation in nutrient regime between the studied mires included in paper II was described using published surface peat elemental concentrations (Olid et al., 2017; Wang et al., 2021), and for two mires included both in papers I and II, we applied the elemental concentrations based on the ICP-OES analyses described above. The elemental data applied in paper II should be considered as rough estimates of variation in nutrient regimes across the mires rather than drivers behind peat accumulation rates in the specific peat cores, since the elemental concentrations in surface peat emanates from separate peat samples than those applied for calculating peat mass (MAR), carbon (CAR) and nitrogen (NAR) accumulation rates.

2.5.3 Generation of mass, carbon and nitrogen accumulation rates

Accurate past (~100 years) peat chronologies for paper II were achieved from the distribution of the natural radionuclide ^{210}Pb (Appleby and Oldfield, 1992).^{210}Pb was determined through the analysis of its granddaughter ^{210}Po, which was assumed to be present in secular equilibrium with ^{210}Pb. For details on the analytical methods, see paper II. Concentrations of excess (unsupported) ^{210}Pb, which is used to generate age-depth models, were determined as the difference between total ^{210}Pb and supported ^{210}Pb. Supported ^{210}Pb was defined as the concentration of ^{210}Pb in the deepest part of the core, where the ^{210}Pb profile became invariant with depth. The ^{210}Pb-based dating was constrained using spheroidal carbonaceous particles (SCP; Swindles et al., 2015) and stable lead isotopes (^{206}Pb and ^{207}Pb) in the peat record to infer independent, supporting, chronological markers in line with techniques described in detail elsewhere for SCPs (Wik and Renberg, 1996) and lead isotopes (Renberg et al., 2001). Finally, cores from Degerö Stormyr and one of the chronosequence mires (S10) were measured for post-bomb ^{14}C to reconstruct the chronology using wiggle matching method (Hua et al., 2022) to further validate the ^{210}Pb derived chronologies.

Peat chronologies of the studied mires were determined using the Constant Flux: Constant Sedimentation (CF:CS) model (Krishnaswamy et al., 1971). In one case the Constant Rate of Supply (CRS) model was applied instead because it provided a MAR that was more consistent with the SCP (Appleby and Oldfield, 1978). In four of the cores neither of the models provided reliable accumulation rates, so mean MAR for these cores were estimated based on the deepest layer where atmospheric ^{210}Pb was found. This depth was divided by one hundred years based on the half-life of ^{210}Pb of around 22.3 years, resulting in a temporal scale of ^{210}Pb of 100-150 years. We multiplied MAR with mean carbon and nitrogen mass-ratios over each peat profile to achieve the mean CAR and NAR over the past 100 years.

2.6 Generation of remote sensing data

2.6.1 Catchment delineation

We described catchment eco-hydrological settings based on a national 2 x 2 m gridded digital elevation model (DEM) generated through LiDAR scanning with 0.5-1 points per square meter, a vertical resolution of 0.3 m, and a horizontal resolution of 0.1 m (The Swedish Mapping, Cadastral and Land Registration Authority). Hydrological modelling was performed using the open-source GIS system Whitebox Geospatial Analysis Tools, SAGA v.7.9.0. (Conrad et al., 2015), as well as ArcGIS v.10.5. We pre-processed the DEM in three steps (Lidberg et al., 2017): first, streams on agricultural land were burned into the DEM; then road and stream intersections were carved into the DEM; and, finally, sinks were removed from the DEM using a breaching algorithm (Lindsay, 2016).

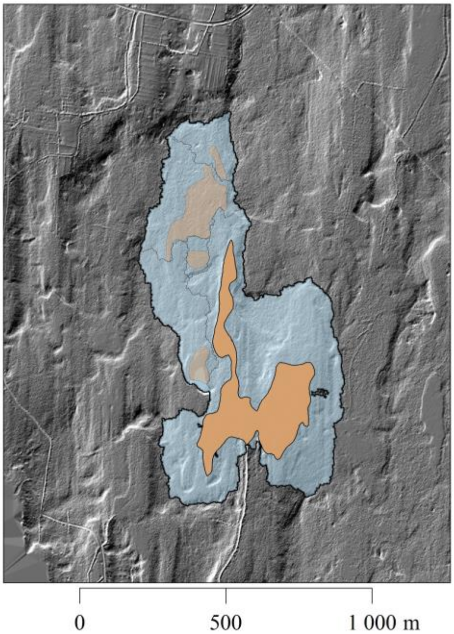

Figure 6. Representation of a mire (brown) with its total catchment area (blue area marked with thick black line) including four upslope mires (shaded brown) with associated unique catchment areas denoted by thin lines. A hillshade map in the background illustrates variation in local topography.

For each mire object, we extracted two upslope catchment areas, the total catchment area (TC) and the unique catchment area (UC), that are hydrologically connected to the mire through flow paths, and which support the mire with water and solutes (Figure 6). The total catchment area includes all upslope areas on mineral soil, including any upslope mires. If mires are found in the total upslope catchment area, they can intercept water and nutrient flows from their upslope areas before these reach a downslope-located mire (Cohen et al., 2016). To describe the upslope contributing area that a downslope-located mire does not share with other mires, we also derived the unique catchment area (UC). In this thesis, I focus mostly on the unique catchment area (papers I-II and IV), as this is considered more effective for nutrient transport to downslope-located mires. For both total and unique catchment areas, we based the catchment delineation on flow direction and flow accumulation maps calculated using the deterministic eight-direction flow model (D8; O'Callaghan and Mark, 1984). Delineation of the total catchment area was based on the original, hydrologically pre-processed DEM (following the steps described above). Delineation of the unique catchment area was instead based on a mire-corrected flow pointer map, on which all mires in the hydrologically pre-processed DEM were assigned the value 0, thus making them hydrological sinks. From the mire-corrected DEM, we calculated flow direction and flow accumulation using the D8 model. For the final catchment delineation, we assigned the entire mire polygon as the catchment outlet. Thus, the contributing area includes all upslope flow paths that pass through the mires. As a final step of catchment delineation, the mire area was excluded from the derived catchment areas, leaving only the contributing upslope catchment area.

2.6.2 Mire and catchment geometry

We described mire-catchment relations based on the areas of the applied mire polygons and areas of the delineated catchment polygons (papers I-II and IV). For specific equations, the reader is referred to the papers. From the mire and upslope catchment areas we calculated the catchment-to-mire ratio, which represents the hydrological catchment support to a mire (papers I-II and IV). A higher ratio suggests that a given mire area is supported by a larger catchment area, representing stronger hydrological support.

While the catchment-to-mire ratio reflects the catchment supply of water to a mire, the ratio between the unique and total catchment areas may reveal biogeochemical catchment controls. For instance, a lower unique-to-total catchment ratio reflects the presence of an upslope-located mire that may have mediated fluxes of water and nutrients across the landscape and acted as a biogeochemical sink to downslope-located mires. For this reason, we calculated the ratio between the unique and total catchment areas (paper I).

We described the two-dimensional complexity of mires shapes using the shape index described by Forman and Gordon (1986). The shape index is based on the quotient between the perimeter of a circle and the true mire perimeter (P) for a given area (A), and thus compares the mire with the simplest possible shape (a circle), which has a shape index of one. The more the index deviates from one, the more the shape deviates from a circle. Using the shape index, mire fragmentation and edge effects can be estimated (Soomers et al., 2013).

2.6.3 Buffers and age zones

The total and unique catchment areas are useful proxies for the regional influence of topography on mires through their hydrological support, but we also extracted 20 m wide 'buffers' (paper IV) to characterise local conditions closest to the mire edge. It is important to consider mire margins because they represent the area up- and downslope of the mire that allows for peat growth and expansion (Ruppel et al., 2013). We also scaled up from the catchment-level to age-zones covering 1 000 years each (paper III-IV), to characterise landscape controls on mire expansion at the wider regional scale, regardless of the individual mire and its surroundings. We defined the age zones based on the 2 x 2 m DEM and the shore displacement curves (Eq.2 in paper III and Eq.1 in paper IV). To represent all non-mire areas that mires could still expand into, we excluded mires from the age zones and described topographic attributes related to the remaining upland areas.

2.6.4 Terrain indices

One of the central indices used in this thesis work is the soil moisture index (SMI; papers I-IV), which colleagues at the Swedish University of Agricultural Sciences have recently developed and which covers most parts of the country (Ågren et al., 2021). This SMI is generated by a machine-learning algorithm based on various terrain attributes at different scales, such as the topographic wetness index (TWI; Beven and Kirkby, 1979), the depth-to-water (Murphy et al., 2011), soil properties, and runoff data. The algorithm was further trained and validated using field data from ~ 20 000 plots. The index describes the likelihood of a pixel being moist, and ranges from 0 (dry) to 100 (moist). The SMI was available as a 2 x 2 m raster. We applied the SMI to identify areas that are sufficiently wet for mire colonisation (paper III), and to describe moisture conditions in the upslope catchment area (papers I-II and IV). Moist areas in the catchment are likely to comprise shallow peat layers which may prevent nutrients from flowing further down the catchment to reach a downslope-located mire. The average peat depth across the catchment area, a derivate from the SMI (Ågren et al., 2022), was calculated for the mires included in paper II.

In contrast to upslope-located catchment areas that were described using the SMI, moisture conditions in the downslope-located mire areas in paper I were described using the topographic wetness index (TWI). We did not use the SMI to describe mire moisture conditions in paper I because the SMI was primarily developed for forests, originally to facilitate forestry operations (Ågren et al., 2021). The commonly used TWI was applied to better describe mire moisture conditions (Beven and Kirkby, 1979). The TWI is based on the slope, representing drainage conditions at the site, and the contributing area, which together describe the propensity of a cell to be saturated at the soil surface. Mires with high TWI scores are likely to be wet due to large contributing areas and gentle slopes, while sites with low TWI scores are expected to be better drained and, as a result, drier. We calculated TWI based on a DEM resampled to a 24 x 24 m resolution, since the TWI performs better when calculated at a coarser resolution (Larson et al., 2022).

One of the most simple, primary terrain indices, which is nonetheless one of the most useful for describing mire development, is terrain slope. We used slope to describe the physical barrier that a mire needs to overcome before expanding further upland (papers IV). In addition, we used slope as a proxy for nutrient transport across the landscape (papers I-II) as steeper slopes are expected to facilitate nutrient transport both from the catchment to the mire (Autio et al., 2020; Kortelainen et al., 2006) and within minerogenic mires from margins to the mire centre (Damman, 1986; Larocue et al., 2016; Rehell et al., 2019). Slope (%) was calculated from the 2 x 2 m DEM according to Zevenbergen and Thorne (1987). High values represent steep slopes.

2.6.5 Catchment land use/cover and geology

We described the catchment land use/land cover, as well as bedrock and Quaternary deposits, using maps available from the Geological Survey of Sweden and the Swedish Mapping, Cadastral, and Land Registration Authority (paper I). The cover (percentage) of each class within the unique catchment areas was used. The following land use/land cover classes (1:10 000) were found according to the map source (Swedish Mapping, Cadastral, and Land Registration Authority): arable land, coniferous forest, deciduous forest, water, and open areas. The following Quaternary deposits (1:100 000) based on the grain size were found in the study area (Geological Survey of Sweden): clay-silt, coarse, sand, and till. Finally, the following bedrock classes (1:50 000) were identified (Geological Survey of Sweden): felsic, felsic-intermediate, intermediate, and mafic.

2.6.6 Vegetation indices

We applied the normalised difference vegetation index (NDVI) to describe vegetation patterns at the mire and sampling point levels in papers I and II. The NDVI is calculated as the difference between the near infrared (NIR) and the visible red wavelengths (Red), divided by the sum of the NIR and Red (Rouse et al., 1973). In Google Earth Engine (GEE; Gorelick et al., 2017), we selected all available Sentinel-2A images with a maximum cloud cover of 30 % over a six-year period (2017-2022) for paper I and a seven-year period (2017-2023) for paper II. For the statistical analysis and modelling, we focused on the vegetation period between May 1 and September 30. However, to illustrate temporal variability in NDVI before and after the vegetation period, we also calculated NDVI for April, October and November in paper I. The Sentinel-2A images were available as 10 x 10 m grids. We masked out pixels covered by clouds (medium and high probability, as well as cirrus), shadows, snow, and ice, or otherwise defect pixels using the Copernicus cloud probability function (Figure 7). The number of images was reduced to one image per month, based on the mean value of all remaining pixels containing NDVI data over the six-year period. Finally, we extracted mean NDVI values and standard deviations for the chronosequence mire polygons. We also calculated monthly mean values for the sampling points included in papers I and II.

In paper I, we distinguished between open and tree-covered mires and open and tree-covered sampling points based on the tree standing volume (m^3 ha^{-1}) described in a 12.5 x 12.5 m national forest map from 2015 (SLU Forest Map. Department of Forest Resource Management, Swedish University of Agricultural Sciences). We classified mires with a median standing volume of 0 m^3 ha^{-1} as open mires, while all other mires were classified as tree-covered. Similarly, we distinguished between open and tree-covered points based on the pixel overlying the sampling points.

Finally, we defined the level of mire drainage in all mires included at the landscape level in paper I based on a national ditch map created using deep learning (Lidberg et al., 2023). The map classifies each 1 x 1 m cell across the landscape into channel or non-channel, including both natural streams and ditches (Laudon et al., 2022). We calculated the total number of stream pixels, normalised it to the mire area, and excluded heavily drained mires with more than 0.02 ditch pixels per square meter, corresponding to > 2 % of the 1 x 1 m pixels across the mire area. After removing heavily drained mires (1 246 mires), the mire population used in paper I comprised 1 576 mire objects that were either undrained (0 ditch pixels per square meter) or moderately drained.

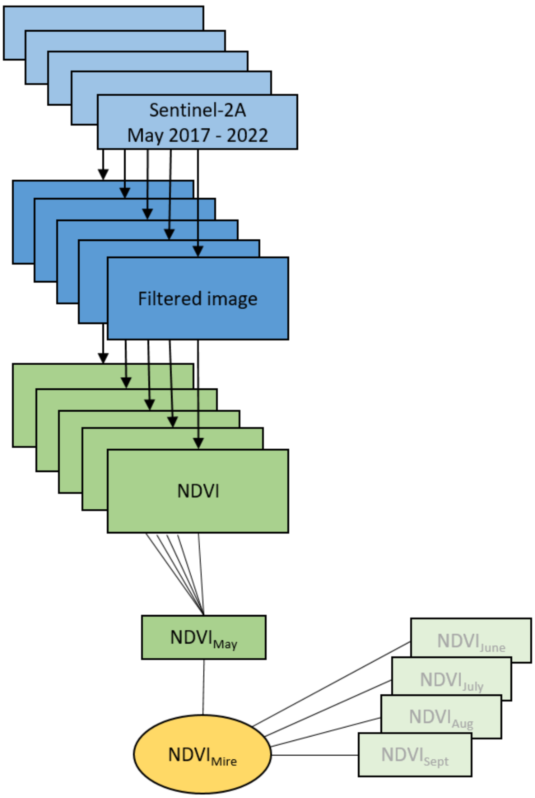

Figure 7. Flowchart showing the extraction of mire level NDVI in May based on Sentinel-2A images processed using Google Earth Engine (paper I). Rectangles refer to maps and the circle represents the mire extent.

2.7 Statistical analysis

2.7.1 Mire pattern distributions over age zones

Mire cover and abundance across the age-gradient of the SMC (papers III-IV), and in the extended BBL region (paper III), are two central landscape properties described in this thesis. We derived these properties by dividing the studied chronosequence(s) into one-thousand-year age-zones based on the land surface age calculated from the shore displacement curves (Eq.1 and Eq.2) and the 2 x 2 m DEM. Before extracting mire cover and abundance, mires on the Swedish property map that were artificially split by roads or ditches were re-aggregated into single mire objects across the chronosequences, since such mire fragments would otherwise be considered as separate mires and, consequently, overstate actual mire abundance. We also considered open water patches within the mire areas to be mire ponds and thus part of the mire area. On the other hand, we treated patches of mineral soil within mire objects as holes in the mire polygons, since they are part of the supporting mineral soil in the mire catchment, which are relevant for our mire-catchment analysis. After preprocessing the mire map, mire cover (%) and abundance (no km^{-2}) were calculated.

To describe the relative areal contribution of individual mires in different age zones over the SMC, we calculated the cumulative mire area relative to the total mire area, the cumulative number of mires relative to the number of mires, and the cumulative number of mires per age zone area. Mires were sorted from smallest to largest before we calculated the cumulative sums. Statistical analyses related to papers III and IV were performed in R version 4.0.3 (R Core Team 2020, Vienna, Austria).

2.7.2 Application of the soil moisture index

To illustrate how the properties of different sized mires change over the age gradient (paper IV), we aggregated mires in the SMC into four area-classes of < 0.01 km^2, 0.01-0.1 km^2, 0.1-1 km^2, and 1.0-10.0 km^2 (note the logarithmic scale). We compared topographic variation in the upslope features (buffers, catchments, and non-mire areas in the landscape-age-classes) as drivers of mire distribution using slope and SMI estimates. For each of the mire area classes, as well as for all upslope features with increasing distance from the mire area and larger spatial scale, we extracted the median and interquartile ranges (IQR = 75^{th} percentile - 25^{th} percentile) of slope and SMI (paper IV).

In paper III, we used the SMI to estimate mire utilisation (%) of suitably wet areas within the ten chronosequences over the 9 000-year age range. We set two moisture thresholds to reclassify the SMI into three classes based on their suitability for mire expansion (Figure 8): moist areas which are highly suitable for mires; semi-moist areas which are drier than the moist areas and less suitable for mires; and, finally, dry areas that are not suitable for mires under present climatic conditions. The thresholds that separate the three classes were defined as the 5^{th} and the 1^{st} percentiles of SMI scores within present mires in each chronosequence (sorted from low to high). Hence, the 5^{th} percentile corresponds to the SMI value that 95 % of all mire pixels match or exceed, separating moist areas from all drier areas (including semi-moist areas), while the 1^{st} percentile corresponds to the SMI score that 99 % of all mires match or exceed, thus separating semi-moist areas from drier areas. The 5^{th} and 1^{st} percentiles were calculated for each chronosequence separately, and medians across all chronosequences were then extracted. The median 5^{th} and 1^{st} percentiles correspond to moisture index scores of 87 and 57 respectively. Here, we refer to areas with an SMI score above 87 as moist, areas with an SMI score above 57 as semi-moist and areas with an SMI score below 57 as dry. As a result, semi-moist areas include all moist areas since these have an SMI score above 57.

Based on the two thresholds applied we identified areas in all chronosequences separately, which had a sufficiently high SMI for mire development. From these, we calculated the mire utilisation (%) of moist and semi-moist areas respectively within each age class in all ten chronosequences. We performed a series of Kendall's rank correlation tests to visually evaluate indications of the existence (and temporal persistence) of a relationship between landscape age and mire utilisation of available areas. To accomplish this, we increased the number of age zones one-by-one in the correlation analysis, starting from the two youngest age zones and moving towards older age zones.

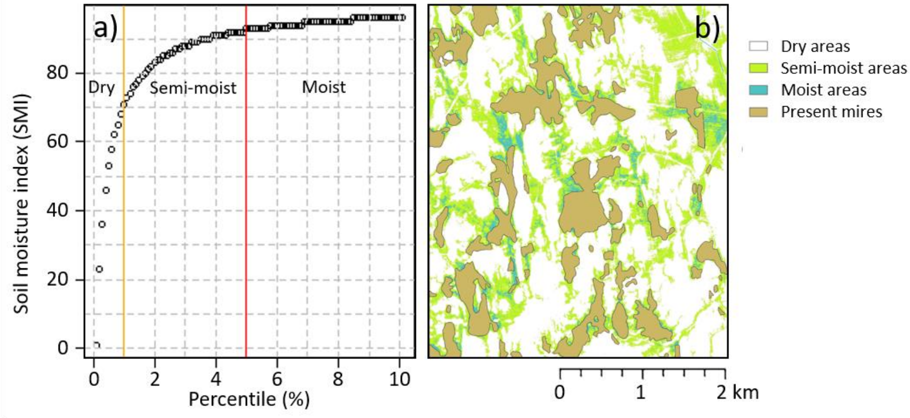

Figure 8. a) Soil moisture index thresholds based on percentiles of the moisture index of present mire pixels in the Sävar rising coastline mire chronosequence (SMC). Vertical lines correspond to the 99th percentile (yellow line) and the 95th percentile (red line). b) The moisture thresholds were used to re-classify non-mire upland areas into dry (white), semi-moist (green), and moist areas (blue). Present mires are shown in brown.

2.7.3 Normalisation to potentially suitable areas

To compare mire lateral expansion based on the potentially mire-suitable areas calculated from the moist and semi-moist areas across all ten chronosequences, we calculated the cumulative mire area relative to the total mire area of each chronosequence (for equations, see paper III). First, we calculated the cumulative mire area as the cumulative sum of mire areas within each age zone starting from the oldest (farthest inland) age zone and moving towards younger (more coastal) age zones. While this calculation generates a simple estimate of the increase in mire area over time, it does not account for differences in the potential for mire expansion introduced by variations in age-zone area. Such variations in land exposure during different periods could result from different isostatic relaxation rates over time and between chronosequences, as well as large-scale differences in slope across the chronosequences. To adjust for this, we derived the cumulative mire-area percentage by rescaling age-zone mire area based on the corresponding age-zone and average age-zone area. Not all areas within an age-zone can be considered equally suitable for mires. Hence, we further normalised the cumulative mire areas based on the occurrence of semi-moist and moist areas. As before, we rescaled mire area using the ratio of mean to age-zone-specific suitable areas and normalised this by the total semi-moist and moist area.

2.7.4 Predicting mire vegetation patterns and accumulation rates

In paper I, the objective was to study catchment controls on mire nutrient regime and vegetation patterns over the past 5 000 years. More specifically, the aim was to identify NDVI and peat nutrient responses to catchment characteristics and landscape aging and, further, to scale up these controls to the landscape level using terrain indices. In paper II, the objective was to identify drivers behind recent peat mass, carbon and nitrogen accumulation rates in lawns and hummocks across an 8 000 year gradient. To achieve this, we used OPLS models (orthogonal projections to latent structures; Eriksson et al., 2006) with one predictive component and one orthogonal component, with the primary focus on the predictive component. The models were generated using the multivariate statistical software SIMCA 17, Umetrics, Umeå (Eriksson et al., 2006).

The OPLS separates variation in the predictive component (x) that is linearly related to the determinant (y) from variation in the predictors (x) that is orthogonal to the determinant (y). Hence, using the OPLS method, variables that co-vary with the determinant can be identified. On the predictive axis of the OPLS model, variables that co-vary with the determinant have high positive or negative loadings on the predictive axis (pq[1]) and are more positively or negatively correlated with the determinant the further away from the origin they are found. Variables with high loadings on the orthogonal axis (poso[1]) are not correlated with the predictor and, consequently, add "noise" to the model. We also calculated the variable importance on projection (VIP) based on the predictive component, to identify variables that were significant for the models. The VIP is normalised such that variables with VIP values greater than 1 are important (Galindo-Prieto et al., 2014).

In paper I, we generated Class-OPLS models for May-September, where open and tree-covered mires were separated as classes. The NDVI was set as the determinant (y), while we defined all other variables as predictors (x). In paper II, we generated separate OPLS models for hummock and lawn accumulation rates, where peat mass, carbon and nitrogen accumulation rates were defined as the determinants (y) in their respective models. In both papers I and II we applied the SIMCA auto-transform function to identify and transform variables that would approach linearity after log-transformation. Apart from applying the predictive OPLS model to the peat accumulation rates (paper II), we also explored co-variation between the accumulation rates and environmental variables using a principal component analysis (PCA).

Flowering bog-rosemary (Swe. rosling, *Andromeda polifolia*)

3. Results and discussion

The discussion presented below emanates from the main findings of the four papers included in this thesis. Its main purpose is to synthesise the results of the papers, with complementary results introduced to support the synthesis. This chapter also covers uncertainties in the data used and their possible impact on thesis outcomes, since the quality and precision of maps and terrain indices applied, and their representation of the ground truth, are central when quantifying, scaling-up, and ultimately conceptualising mire-landscape interactions. The results are presented from a mire-development perspective, starting by describing how catchments control the inflow of nutrients to mires and how this is manifested in the mires' nutrient regime and vegetation patterns (paper I). From there, I move on to describe how accumulation of peat, carbon and nitrogen vary over temporal and spatial scales (paper II), and finally, I discuss how mires expand laterally depending on local moisture conditions (paper III) and how the catchment and wider surrounding landscape influence mire patch distributions (paper IV).

3.1 Controls on mire vegetation patterns (paper I)

In paper I, we hypothesised that variation in mire nutrient regime is reflected in mire vegetation patterns as described using the remotely sensed NDVI. Based on our models, we were able to confirm this hypothesis (Figure 9). Specifically, peat concentrations of phosphorus and potassium were strong predictors of NDVI. In the case of phosphorus, variation on the orthogonal axis, which represents variation that is not related to the NDVI, was almost zero. This is probably because mire plants immediately take up any phosphorus that is released from the inaccessible peat pool (Bombonato et al., 2010; Kellogg and Bridgham, 2003), resulting in a strong co-variation between phosphorus concentrations and NDVI. Potassium, in turn, is one of the most mobile elements in peat (van der Heijden et al., 2017), with only weak bounds to the cation exchange complex (McCarter et al., 2021). We interpreted the co-variation between potassium and NDVI as a direct vegetation response to more nutrient-rich conditions at the mire surface. In addition to phosphorus and potassium, different combinations of electrical conductivity, dry matter content, and nickel, magnesium, manganese, and zinc concentrations were associated with NDVI, depending on the month.

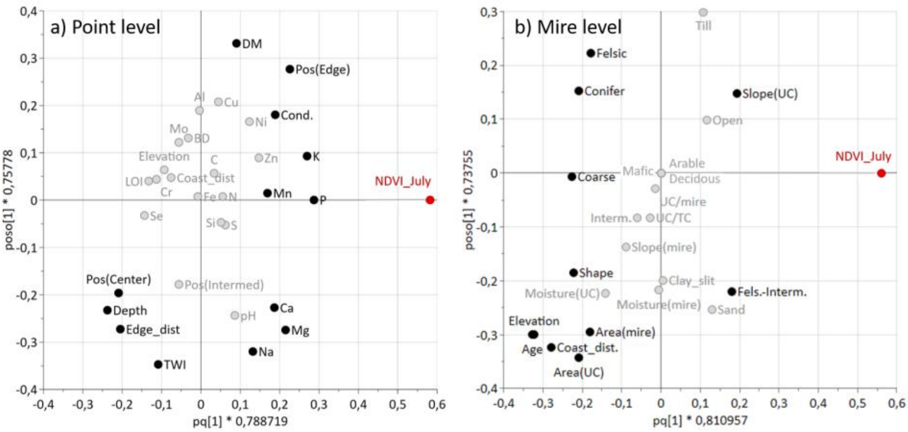

Figure 9. OPLS models for the normalised difference vegetation index (NDVI) for open mires at the sampling point (a) and mire (b) levels during peak season (July; paper I). Variables in black are significant and variables in grey non-significant according to the predictive VIP scores (variable importance on projection).

We based our models in papers I-II on elemental concentrations in peat, since we consider the solid peat phase to be a more constant long-term archive of nutrients than, for example, pore water concentrations (Chambers and Charman, 2004), hence they are more representative of the nutrient regime at a site. However, as part of the sampling procedure related to paper I, I also collected green aboveground tissue (leaves) from six plant species that were expected to be abundant across the age and nutrient gradients of the SMC. Absolute plant concentrations were around two times higher for phosphorus and ten times higher for potassium when compared with peat concentrations but, despite this, we found indications of nutrient gradients between the mire edges and centres both for surface peat and plants. This further confirms that not only do elemental concentrations in peat vary with horizontal distance to mineral soil, as described in paper I, but so do plant concentrations. Our motivation for using peat instead of plant concentrations in paper I was that plant nutrient-use efficiency is largely dependent on nutrient availability (Bridgham et al., 1995), hence the uptake of nutrients may be selective dependent on diffusion rates. Furthermore, the co-existence of different mire plant species may depend on plant traits (Moor et al., 2017), as well as on plant-microbe interactions (Robroek et al., 2021). Based on this, we considered peat elemental concentrations to be more robust than plant elemental concentrations as catchment signals. In addition, from a practical perspective, not all plant species were present at all sampling locations so using plant samples rather than peat samples could have resulted in poorer representation of gradients in age, nutrient regime, and catchment eco-hydrological settings over the SMC.

Scaling up from the sampling point level to the mire level and, further, to the entire mire population at the landscape level advanced our understanding of how mineral nutrients released by weathering from the surrounding and underlying mineral soils are transported to the mire surface through surface or groundwater flow paths (Figure 1), and how mire vegetation responds to this. For tree-covered mires, the tree standing volume correlated positively with NDVI and was the dominating driver of NDVI.

We found that older mires, with a greater distance between the mire surface and mineral soil both vertically and horizontally, were associated with lower NDVI, or less productive conditions. To support this, we also found mire margin-expanse gradients (Korpela and Reinikainen, 1996) representing higher NDVI close to the mire margins than in the expanses. Efficient immobilisation of nutrients resulting from their uptake by mire plants, as well as limited transport of nutrients over the mire surface, may explain the observed gradient in open mires, while a denser canopy cover close to mire edges was probably the main driver of NDVI edge effects observed in tree-covered mires. At the larger spatial scales, variables describing mire and landscape age were similarly associated with lower NDVI both for open and tree-covered mires over most of the studied months. Mire age may result in lower NDVI for two distinct reasons. Firstly, older mires represent mires with deeper peat layers (Figure 11), and thus weaker support of nutrients from underlying mineral soil (Hughes and Barber, 2004). Secondly, nutrient gradients formed by easily weatherable minerals form strong nutrient gradients across the aging landscape, with lower transport of nutrients to older mires (Starr and Lindroos, 2006). Whether either of these are the main driver, or they both contribute equally to the observed nutrient depletion in older mires, remains to be explored.

Aside from nutrient gradients associated with weathering rates, the transport of nutrients from upslope catchment areas to mires largely depends on local topography. We found indications that catchment slope and moisture restricted nutrient transport to mires at least during parts of the vegetation period, such that flat catchments prevented water and nutrients from reaching downslope-located mires (Autio et al., 2020; Kortelainen et al., 2006). On the other hand, a very steep catchment can result in more nutrient-poor minerogenic water reaching the mire, due to shorter contact time between soil water and mineral soil (Maher, 2010). A large catchment-to-mire ratio was positively correlated to NDVI in tree-covered mires, which further confirms the role of catchment in transporting nutrients to mires. On the other hand, larger mires were associated with lower NDVI, probably because of insufficient nutrient support to sustain a high NPP across the mire surface.

In open mires, moister conditions at the mire surface and in the upslope catchment area were associated with lower NDVI during green-up and senescence. Similarly, at the sampling point level we also found that wetter conditions at the mire surface were associated with lower NDVI during all months (May-September) in tree-covered sampling points and during green-up (May) and senescence (September) in open sampling points. Lower NPP under wet mire conditions was most likely due to inundation, which restricts mire productivity (Balliston and Price, 2022), but dilution of elements may also have resulted in lower concentrations of plant-available nutrients (Ågren et al., 2012; Eppinga et al., 2010). Similarly, steeper sloping mire surfaces were positively correlated with NDVI in open mires during green-up and senescence, and catchment slope correlated positively with open mire NDVI during all months except August. If the mire slope direction is favourable, a steeper slope may result in more even nutrient distributions across the mire surface and result in more even vegetation patterns (Damman, 1986; Larocque et al., 2016; Rehell et al., 2019).

3.2 Variation in vertical accumulation rates (paper II)

In sites with favourable hydrological and nutrient conditions (paper I), mire plants may become peat accumulating (Rydin and Jeglum, 2013). We found recent peat mass (MAR) and carbon accumulation rates (CAR) to increase over the studied age gradient of around 8 000 years, and with increased peat depth, despite the absence of systematic changes in the water table depth (Figure 10; paper II). MAR and CAR were initially lower in young hummocks compared to lawns, but because the increase in accumulation rates over time was faster in hummocks than in lawns, MAR and CAR in hummocks exceeded that of lawns after around 4 000 years of land exposure.

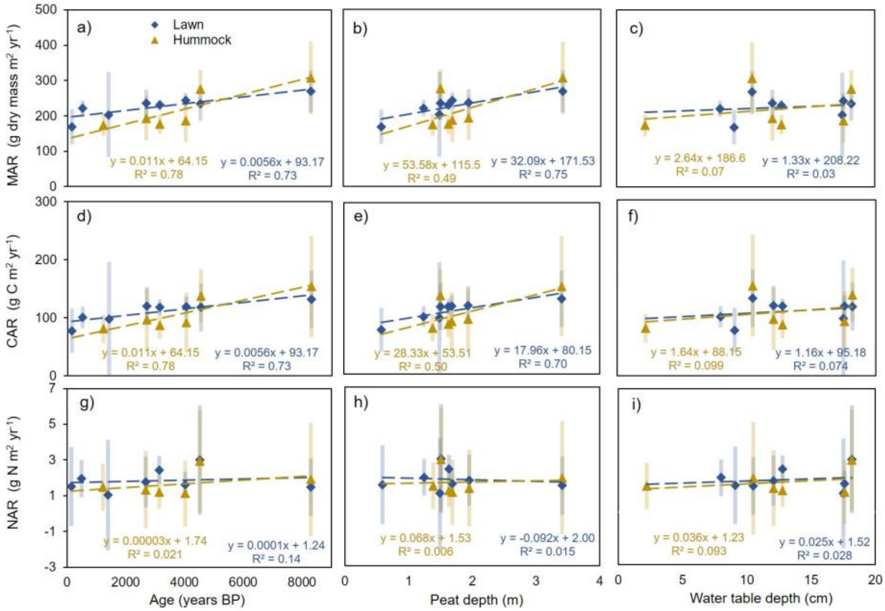

Figure 10. Accumulation rates of peat mass (MAR; top), carbon (CAR; mid), and nitrogen (NAR; bottom) in lawns (blue) and hummocks (yellow) in response to mire ages (left), peat depths (mid), and water table levels (right).

Nutrient availability determines plant community composition, and thus the NPP at a particular location (Økland et al., 2001). Importantly, however, nutrient-rich mires have higher NPP (paper I), but may accumulate peat slower than more nutrient-poor mires, because decomposition is also higher with high nutrient availability (Damman, 1996; Szumigalski and Bayley, 1996). We found indications that groundwater had such a negative impact on

MAR and CAR in the studied mires (paper II). We drew this conclusion from the negative co-variation between recent MAR and CAR on the one hand, and surface peat concentrations of silicon, iron, and magnesium on the other hand, all of which are associated with higher groundwater inputs. As in paper I, we found the NDVI to co-vary with a higher peat nutrient supply (paper II), but despite this, the NDVI was not significant in any of the models predicting accumulation rates, which further supports the theory that it is the decompositions term that is stimulated by increased ground water influence.

While MAR and CAR were negatively influenced by the support of weathering-derived nutrients from the upslope catchment area or underlying mineral soils, we found nitrogen accumulation rates (NAR) to be supported by minerogenic water inputs (paper II). We concluded this from the positive co-variation between NAR and peat concentrations of potassium, manganese, calcium, and aluminium. Importantly, iron concentrations in peat were also positively correlated with NAR (paper II). Iron is a cofactor in all three nitrogenase enzymes responsible for nitrogen fixation and is known to stimulate nitrogen fixation (Larmola et al., 2014).

Estimations of recent peat accumulation rates from ^{210}Pb chronologies cover the past 100-150 years and often, as in the case of paper II, include the seasonally aerobic acrotelm layer close to the mire surface. In the unsaturated acrotelm, aerobic decay is much faster than that which is possible in the anaerobic catotelm. Since the acrotelm-catotelm transition of peat, which is a prerequisite for the long-term rate of peat accumulation, depends on variation in the decomposition term, short-term CAR does not directly reflect long-term rates (Young et al., 2019). For example, in Degerö Stormyr the short-term CAR calculated in paper II were up to ten times higher (lawn: 132 g m^{-2} yr^{-1} and hummock: 154 g m^{-2} yr^{-1}) than the long-term CAR of 13.7 g m^{-2} yr^{-1} (Larsson et al., 2017). The short-term rates calculates in paper II were, however, similar to earlier reported rates from the mire (Olid et al., 2014).

Using the chronosequence approach, we can compare recent peat accumulation rates with a rough peat height growth rate (PGR). By dividing the maximum peat depth measured at a peat sampling site with the mire age estimated from the elevation (mire bottom), we get an estimate of the average peat height increase since mire initiation. As well as sampling points included in paper II (Figure 11c), I have applied this calculation to all sampling points visited for paper I (Figure 11b), including sampling points at mire margins (N=160), intermediate positions (N=160), and in the centre of mires (N=80). PGR varied between mire edges and centres, as expected, due to differences in aeration, compaction, and basin depths at these locations (Figure 11). Overall, however, peat depth increased over time regardless of location across the sampling transect. In young mires, PGR was high (over 5 mm yr^{-1}), but over the first ~ 1 000 years PGR slowed down to stabilise at < 1 mm yr^{-1}. This was consistent across the sampled mires. In young mires, peat is less compacted than in older mires, which probably explains the decrease in PGR over time.

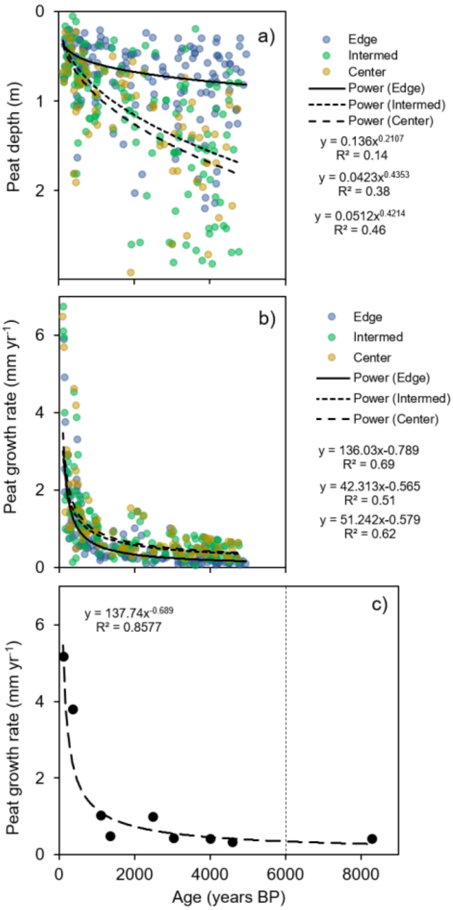

Figure 11. a) Depths by mire margins (N = 160, blue), as well as intermediate (N =160, green) and central (N = 80, yellow) positions over the past 6 000 years in mires visited for paper I. b) Average peat height growth rates since peat initiation estimated from peat depth, and mire bottom age estimated from the elevation above sea level and a local shore displacement curve (Renberg and Segerström, 1981) over the past 6 000 years. c) Peat height growth rates over the past 8 000 years for mires included in paper II.

3.3 Moisture controls on lateral expansion (paper III)

As dead plant materials start accumulating (paper II), they may initiate mire formation, which can in turn result in expansion vertically (Figures 10-11) or laterally (papers III and IV) depending on local topographic and hydrological conditions in combination with biomass production rates and subsequent peat accumulation rates. In paper III, we studied hydrological constraints to mire lateral expansion over ten mire chronosequences (~ 5500 km^2) along the coastal areas of the Bothnian Bay Lowlands (BBL).

We found that the availability of moist and semi-moist areas determined mire coverage over time (Figure 12). Mire colonisation of moist areas was rapid compared to the utilisation of semi-moist areas: within ~ 2 000 years after land exposure from the sea, mires reached maximum utilisation of moist areas, at 70-80 %, with almost no further utilisation thereafter. This confirms that the fast lateral expansion rates in flat areas that have sporadically been reported for individual mires elsewhere (Korhola, 1994), also applies to the wider mire landscape. Interestingly, this timing also coincides with the levelling out of PGR (Figure 11), which suggests that there is a certain degree of commonality in the timing of vertical and lateral peat expansion.

For semi-moist areas, the increase in mire cover was slower and continued over the first ~ 4 000 years, finally reaching a maximum utilisation of less than 40 %. We cannot say for certain when mire expansion occurred within this 4 000 year period or, in the case of moist areas, over the ~ 2 000 years reported, only that land suitable for mire utilisation was colonised to the same degree across the studied chronosequences. After this time, suitable areas needed to become wetter, for instance through changes in the climate, for the mires to expand further laterally. Importantly, we found that neither the moist nor the semi-moist areas approached 100 % occupation by mires. Drainage of mires has caused a loss of mire areas in the northern Swedish landscape, but drainage of upland areas has also led to changed flow paths, which have influenced the applied soil moisture index. This may partly explain the gap in utilisation of available areas. Apart from this, a natural bi-stability between mires and forests occurs, such that both ecosystems can occupy the same locations and modify local hydrology to suit their vegetation and growth (Ohlson et al., 2001; Ratcliffe et al., 2017; Velde et al., 2021).

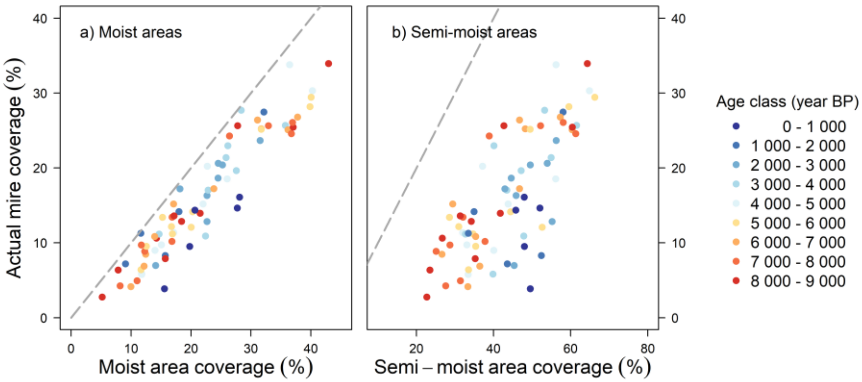

Figure 12. a) Contemporary mire coverage across ten mire chronosequences compared to mire available moist (a) and semi-moist (b) land areas. Points represent 1 000-year age-zones where a bluer colour corresponds to a younger landscape age and a redder colour corresponds to an older landscape age. For interpretation, the 1:1 line is marked, which corresponds to the hypothetical scenario where all hydrologically suitable land areas are occupied by mires.

As we normalised cumulative mire coverage curves to the mire-available moist areas in each age zone, all studied chronosequences approached linear-like expansion rates (Figure 13). However, based on the variation in expansion rates that still remained after normalisation to moist areas, we outlined three possible patterns of mire lateral expansion in the BBL. For the first of these, we compared the chronosequences to the hypothetical zero-expansion curve, in other words a trajectory of linear mire increase over time. Such a trajectory would arise if cumulative mire area increase were only caused by isostatic relaxation and the continuous emergence of 'new' land areas. Five of the studied mire chronosequences oscillated around the zero-expansion curve (Haparanda, Kalix, Luleå, Piteå, and Sävar). The second pattern emerged as follows: if a landscape was not defined by any local topographic constraints, and peat accumulated at a constant rate, the cumulative mire area would increase more slowly in younger age classes and faster in older age classes because of the continuously increasing mire area. This would result in cumulative curves above the hypothetical zero expansion curve. Two of the studied mire chronosequences experienced such expansion (Byske and Skellefteå). The third trajectory relates to average, long-term changes in peat accumulation rates over time. If peat accumulation rates were initially fast, but gradually slowed down over the course of mire development (Figure 13), in contrast to the vertical expansion rates found for the SMC (paper II), the cumulative curves would lie below the hypothetical zero line. Three of the chronosequences showed this pattern (Robertsfors, Hörnefors, and Nordmaling). In this context, it is important to remember the difference between recent and long-term peat accumulation rates as influenced by different peat decomposition rates. Based on these differences, the results of paper IV, showing increasing recent peat accumulation rates over time in the SMC, and the third trajectory of long-term peat lateral expansion are not necessary contradictory.

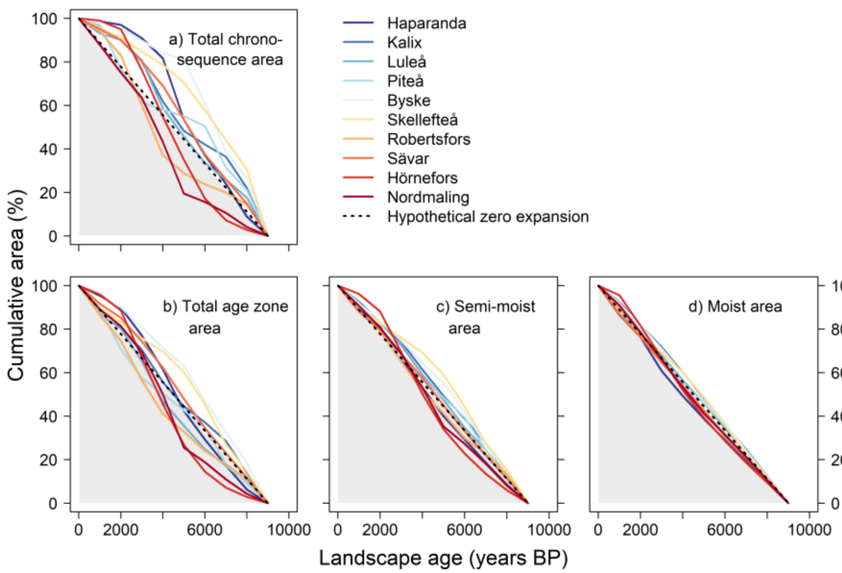

Figure 13. Cumulative mire area normalised relative to a.) total chronosequence specific land area, b.) specific age zone area, c.) semi-moist areas, and d.) moist areas within the age zones. When equally large mire areas are added for each age class, i.e. no lateral expansion occurs, cumulative mire area results in the marked hypothetical zero expansion line. Chronosequences above the line experience larger areal increase in older age zones, due to constant lateral expansion rates, but increased mire area over time or faster mire lateral expansion in older age zones. Chronosequences below the hypothetical zero expansion curve, in the grey shaded area, experience faster lateral expansion in young or intermediate age zones than in older age zones.

3.4 Catchment drivers of mire morphology (paper IV)

As mires initiate and expand, depending on local hydrology (paper III), they will eventually generate mire patch distributions typical of the boreal landscape (paper IV). Mire morphology and patch distributions may reveal controls on mire initiation, lateral expansion, and possibly on the merging of smaller mire segments into large mire complexes. We found two main mire morphological groups that were present across most parts of the SMC (paper IV). The first group consisted of small mires with relatively simple shapes, which were present across all age zones up to 9 000 years. The second group consisted of larger mires that emerged after around 1 000 years, which had more complex shapes. These mire complexes accounted for a large portion of the total mire area in the SMC. For example, in the 6 000-year landscape age class the six largest mires out of the total of ~ 260 mires accounted for some 66 % of the mire area within that age class.

Established mires formed through primary mire formation may expand laterally over time after establishing sufficient peat accumulation rates (paper II) while, in contrast, peat initiation through paludification or terrestrialisation may lag behind land availability and continue to form in the aging landscape. Furthermore, terrestrialisation is often less reliant on water inputs from the surrounding landscape because of the continuous saturation of peat from the underlying water lens which shrinks over time. Likewise, mire initiation through terrestrialisation can proceed during drier periods when primary mire formation and paludification are restricted (Ruppel et al., 2013). This probably accounts for the observed differences in mire shapes, such that small mires in the youngest parts of the landscape were more variable in terms of shape complexity than small mires in older landscapes. In young parts of the SMC primary mire formation has probably been the dominant initiation pathway, similar to the situation in land-uplift shores on the Finnish side of the Bothnian Bay (Huikari, 1956). Here, mire initiation along bays may lead to more complex shapes than paludification in flatter terrestrial areas later in history. However, as mire lateral expansion proceeds, the shapes of mires formed through primary mire formation and terrestrialisation are likely to remain simple, and partly restricted to the original basin, while continuous expansion through paludification on flat areas may potentially result in shapes that are more complex. Specific drivers behind these two identified morphological groups remain to be studied.

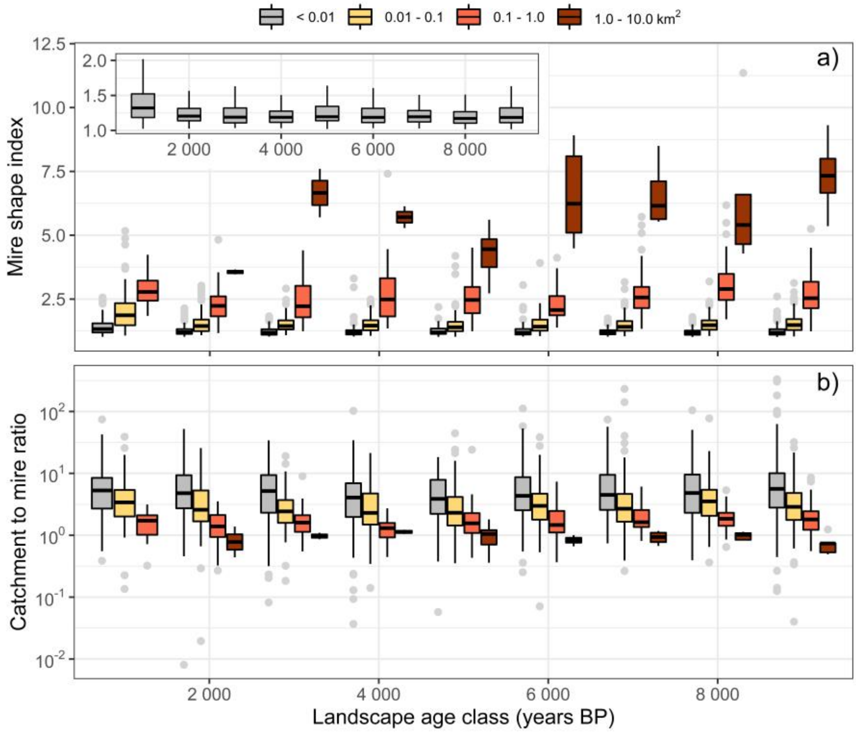

Figure 14. Mire shape index (a) and catchment-to-mire area (b) in different mire area groups (0 - 0.01 km^2, 0.01 - 0.1 km^2, 0.1 - 1 km^2 and 1.0 - 10.0 km^2). In panel (a) the smallest area group is displayed (without outliers) in the plot inset. The catchment-to-mire ratio (note the logarithmic scale) was based on the unique upslope catchment area, which a mire does not share with any upslope mire.

We explored variation in the catchment-to-mire ratio over time and over mire area groups, since this ratio should define the persistence of the mire area in minerogenic systems (Sallinen et al., 2023). We found a decrease in the catchment-to-mire area as mire area increased, which was expected as mires grow into the constant topographically-defined catchment area, with the ratio stabilising at ~ 1:1 (Figure 14). Small mires were more variable regarding their catchment-to-mire ratios, which indicates that these systems may tolerate a wider range of hydrological conditions than larger mires do. However, mires with a higher catchment-to-mire ratio are likely to be more resilient to drought than those with weaker catchment support (Lambert et al., 2022). A mire with weak support, either originally based on the topography or after time due to lateral expansion beyond the hydrological support capacity of the catchment, may risk drought and potentially loss of mire area (Gallego-Sala and Prentice, 2013; Velde et al., 2021). It is important to keep in mind, though, that mires may maintain a high water level even under less favourable or fluctuating groundwater conditions (van Breemen, 1995). Hence, both the catchment and a mire's internal control on its water level are likely to affect the vulnerability of minerogenic mires to changed hydrological conditions (Lambert et al., 2022).

In addition to the total catchment area, slope and moisture conditions at the catchment and buffer levels represented topo-edaphic controls on mire expansion and defined mire morphometry (paper IV), much in line with our findings at the larger landscape level (paper III). Mires in the SMC were found on slopes of up to ~ 4 % (~ 2° slope). Supporting upland areas (catchments and buffers) represented surfaces with slopes of more than 4 %, but also some surfaces with lower slopes (> 2 %). The slope limit in the SMC is higher than those reported for southern Sweden (Almquist-Jacobson and Foster, 1995), but lower than slopes in wetter parts of the country, probably depending on the local water balance (Ivanov, 1981). For example, in wetter parts of Sweden such as the west of the province of Dalarna, mires commonly cover slopes of 5-10 %, and up to 14 % in some areas (Rydin et al., 1999). Interestingly, we found that small mires were in general steeper than larger mires. Whether this reflects differences in total peat accumulation and 'smoothing' of the underlying topography (Loisel et al., 2013), or that small and large mires have formed in different parts of the landscape, this study cannot answer.

After ~ 5 000 years, slopes in areas closest to the mire margin (buffers) became increasingly steep, which suggests that mires in older parts of the landscape face increasing topographic constraints over time. The low catchment and buffer slopes found in younger parts of the landscape suggest that the small total mire area in young parts of the SMC must reflect constraints that are not defined by local topography, but rather by temporal factors related to the timing and spread of mire initiation or the rate of lateral expansion (Ruppel et al., 2013). In parts of the chronosequence that have been exposed for less than 1 000 years, mire initiation may have been restricted by the relatively short time that the land has been exposed from the sea. Importantly, slopes in the buffers were not sensitive to the applied buffer width. In contrast to results at the age zone level (paper III), we found that upland moisture conditions (in catchments and buffers) increased with landscape age, especially in the 0-5 000 years BP range. This probably reflects the build-up of humus or shallow peat layers surrounding the mires (Ågren et al., 2022).

To further compare mire morphology in the SMC with the wider mire landscape of the BBL, I compared mire coverage (%) in each 1 000-year age zone of the ten mire chronosequences applied in paper III (Haparanda-Nordmaling) with the distribution of mires within the age zone. Distribution here refers to the number of mires per mire area in each age zone. Taken together, across the BBL, low mire coverage is associated with small-scattered mires, while higher coverage is associated with fewer and larger mires (Figure 15). This trend was consistent across the BBL, although the individual chronosequences partly represented different sections of the curve. For example, the SMC represented more-or-less average mire coverage, but the distribution of mires was slightly more scattered than that of the other nine chronosequences.

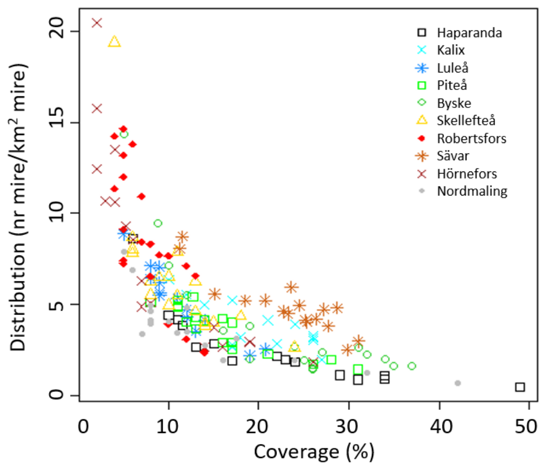

Figure 15. Mire cover (%) compared to the distribution of mires (number of mires per square kilometre of mire area) in each age zone.

3.5 Summary and implications

3.5.1 Development of mire functions over spatial and temporal scales

The functions and ecosystem services provided by high-latitude, minerogenic mires largely depend on the morphology and arrangement of mires described in this thesis (paper I-IV). However, through their hydrological connection to the surrounding boreal landscape, mire processes have a much wider influence on the boreal landscape mosaic as a whole (Belyea and Baird, 2006; Sjöström et al., 2020).

In young, coastal parts of the SMC, small scattered mires have systematically shallower layers of accumulated peat (paper I), hence a shorter vertical distance to underlying mineral soil, than is found in mires in older parts of the landscape. At the same time, upland mineral soils in younger parts of the landscape still contain easily weatherable minerals that can release nutrients for transport to downslope-located mires (Hoffland et al., 2002; Starr and Lindroos, 2006). These two circumstances have resulted in more nutrient-rich (Wang et al., 2020) and productive mire ecosystems (paper I) in the young parts of the chronosequence.

Following from this, mires in younger parts of the chronosequence contribute more to higher plant biodiversity (Laine et al., 2021b) and regulation of various biogeochemical processes (Wang et al., 2021). However, we have been able to show that old parts of the chronosequence are characterised by a heterogenous mixture of different sized mires, which might benefit biodiversity at a landscape level if plant species richness is greater with smaller patch sizes or complexes of laterally merged mires with advanced mire shapes and stronger edge effects (Howie and Meerveld, 2011). For northern European peatland birds, open areas and low tree height are often beneficial (Fraixedas et al., 2017), so birds may also be favoured by the (older) larger chronosequence mires.

In contrast to our results on short-term CAR (paper II), which suggested higher accumulation rates in older mires, long-term CAR in young minerogenic mires is often much faster than that in older mires (Ratcliffe et al., 2018; Tolonen and Turunen, 1996), as is also shown by their respective peat increment rates (Figure 11). In fact, old mires may be close to carbon neutral, with accumulation rates around zero (Mäkilä et al., 2001). Meanwhile, *Sphagnum* dominated mires may grow faster vertically than mires with other vegetation types if such growth is limited by phosphorus and nitrogen, since *Sphagnum* moss has a very low requirement for these nutrients (Heinselman, 1970).

When it comes to the total carbon store, spatially extensive, old mire complexes represent larger peat carbon stores than small-scattered mires, as the peat carbon store directly depends on mire area and depth, meaning that a larger mire basin can support a larger peat carbon store (Figures 10-11). Importantly, though, if mire expansion in flat areas has been rapid (Loisel et al., 2013), some of the areas within a large mire complex might have rather shallow peat layers, and thus represent smaller carbon stores per unit area. It is also important to note that in many cases the development of large mire complexes cannot be described as a unidirectional process, since peat may have expanded at varying rates (paper III; Ruppel et al., 2013) and different mire types may have replaced each other in site-specific ways that do not follow the classic fen-bog transition (Heinselman, 1970).

Edge effects may also result in lower CAR due to better aeration, hence decomposition, at mire edges (Nordström et al., 2022). Most of the 80 mire transects in the SMC that were visited as part of this thesis work had relatively steep sloping edges, as measured every 2 m from the estimated mire edge to the first sampling point (Figure 16). In such cases, with regards to the peat carbon store, edge effects are likely to be rather limited.

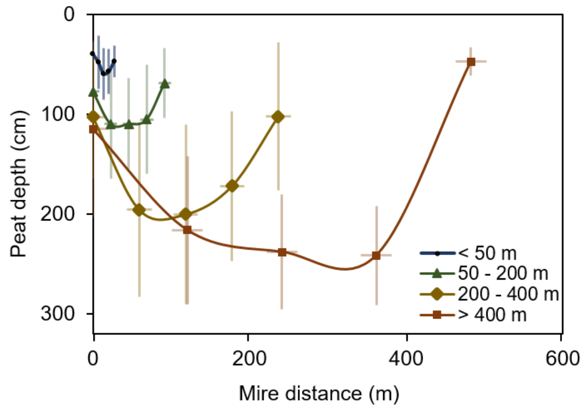

Figure 16. Mire depth profiles across all mire transects sampled as a part of fieldwork related to paper I.

Under certain conditions, the aging and succession of mires through peat accumulation over the course of their development may lead to a shift from minerogenic to ombrogenic conditions, sometimes referred to as ‘ombrotrophication’ (Väliranta et al., 2017). This term is useful, for instance when describing the increasing mire surface convexity that occurs over time in raised bogs (Clymo, 1984) and the decreased inflow of nutrients from the surrounding catchment area which often results in a shift from sedge- and forb-dominated plant communities to moss-dominated plant communities (Kolari and Tahvanainen, 2023). However, from a hydrological perspective, the term 'ombrotrophication' should be used with caution as, although a mire may lose its hydrological support from the upslope catchment area when its surface rises above its margins, it may still receive minerogenic water and nutrients from deep groundwater intrusions (Jaros et al., 2019), even if little of this water reaches the mire surface. In addition, true fen-to-bog transitions are restricted to areas with a sufficiently long vegetation period and enough precipitation (Almquist-Jacobson and Foster, 1995; Damman, 1986; Granlund, 1932), which excludes the possibility of ‘ombrotrophication’ in many high-latitude landscapes.

Across the studied chronosequence, catchment-to-mire ratios decreased as mires expanded upland (paper IV), but even the largest mire complexes were still associated with a contributing catchment area, thus making them minerogenic but often oligotrophic. The observed increase in MAR and CAR from decreased groundwater through-flow (paper II) is also opposite to what would be expected from ombrogenic mires, which further suggests that oligotrophication, rather than ombrotrophication, is the main process leading to more nutrient-poor conditions in the surface peat in inland parts of the SMC.

3.5.2 Past, present and future studies on mire-landscape interactions

I would like to come back to the quote by Påsse and Daniels (2015), which I cited at the beginning of this thesis: ‘*A human lifetime is so short that we usually do not appreciate changes occurring in the landscape*’. This quote was originally used to describe the rapid shore displacement along the northern coast of Sweden (which has given rise to the mire chronosequence studied in this thesis) and its modification of seashores that are noticeable even within a human lifetime. However, with this quote in mind, and the fact that human livelihoods in northern Sweden have depended on forests and forest products, even more so in the past than today, it is understandable that the lateral expansion of mires in inland and coastal areas worried past landowners and researchers.

In the early 1900s, the term 'swampification' (Swe. försumpning) was used to describe lateral expansion of peat into productive forests which, in northern Sweden, was generally thought to result from water flowing from more central parts of the mire to the mire margins, and eventually to surrounding upland areas. The first doctoral thesis (Malmström, 1923) carried out in the now widely-studied Degerö Stormyr challenged this notion of 'swampification'. Carl Malmström suggested that the wetting of mire margins, and lateral peat expansion resulting from it, depends on the inflow of water from upland areas, rather than the reverse. Through his thesis, Malmström disproved the risk of 'swampification' in northern Sweden.

It is with great pleasure that I, exactly a hundred years after Malmström's work, can test similar ideas about long-term mire development in the same region, only now in the light of mire-upland interactions and at the landscape level. Despite obvious differences in methods, scales, and references, it is striking to note how many of Malmström's ideas still apply, even at much larger spatial scales than he addressed in his original work.

Today, 'swampification' is no longer considered a threat to northern Swedish forests. In contrast, the loss of mire area through drainage is a more serious threat to northern mire landscapes. Beyond this, high-latitude mires' role in climate change is a significant current concern. It is vital that future studies explore questions relating to how changed hydrological conditions will influence the balance between peat accumulation and decomposition rates and water and nutrient inflows to mires. Will a warmer future climate result in oxidation and decomposition of old peat, and can we mitigate the carbon fluxes that would follow from this? Rewetting of managed peatlands has gained increased interest in Sweden, and globally, over the past few decades. It will be important to assess how efficient rewetting actions intended to preserve carbon that is locked up in peat actually are, and whether the catchment area should be considered when minerogenic mires are rewetted. These are examples of some of the concerns that will need focused attention, to better understand mires' and their catchments' roles in a warmer future climate.

3.6 Uncertainties and their impacts on thesis outcomes

3.6.1 Land use in the mire and upslope catchment area

Before concluding this thesis, I would like to acknowledge a few uncertainties related to the data used. Firstly, land-use factors are known to modify present mire area, connectivity between mires, and the broader landscape mosaic in high-latitude landscapes (Fergus et al., 2017). Over the past 250 years or more, haymaking on mire meadows and drainage for agricultural or forestry purposes have been the main land-uses on mires in the region (Norstedt et al., 2021). In general, the loss of open and, from a forestry perspective, un-productive mires is likely to be unimportant compared to the loss of tree-covered mires. This is because most mire drainage activities have been focused on peatlands that were already covered by sparse tree-cover prior to drainage and had a higher potential to become productive forests than did open mires.

The potential loss of mire area in the SMC due to drainage may have influenced our results and interpretations of drivers behind mire distribution patterns, particularly in paper III. Importantly, however, our main focus has been on open and sparsely treed mires, which are likely less to have been affected by drainage activities. While exploitation of mires from different land-use activities has affected present-day mire extent, as shown in the mire map, direct effects on the landscape-level results of this thesis (papers I and III-IV) mainly relate to the lateral expansion of mires. At the individual mire level (papers I-II), the impact of potential loss of mire area on our results is likely to be minor, but these results could also be affected by land-use changes if, for example, mire margins have been drained, resulting in drier conditions by the mire margins and accelerated peat decomposition rates. Human-induced land-use changes in the upslope catchment area may also reduce the inflow of water and nutrients to minerogenic mires, causing oligotrophication, if changed flowpaths disconnect a mire from its nutrient-supporting catchment area. Drainage at mire margins, or higher up in the catchment, may cause such oligotrophication (Tahvanainen, 2011), although the impacts of human-induced oligotrophication on mires' nutrient regimes remain unclear.

3.6.2 Mire and age zone accuracy

We used an aerial photo-based mire map to describe present-day mires in the SMC (papers I and III-IV) and in the additional nine chronosequences along the BBL (paper III). Generally, the mire map is accurate for large (> 2 500 m^2) mires, while smaller mires have been only sporadically mapped. In addition, open and sparsely treed mires have been relatively well mapped, while the accuracy of mires with denser canopy cover is poorer, particularly in terms of the exact position of the edges of mires with diffuse edge zones. Consequently, moist and semi-moist areas that we considered unutilised (paper III), might in some cases constitute diffuse mire edge zones with varying peat depths. The results of paper III thus mainly describe lateral, and therefore because of the chronosequence approach also temporal, dynamics of mires that have remained open or sparsely treed since their initiation and expansion.

Under certain conditions, the timing of the initiation of individual mires may be over-estimated using the chronosequence approach, as mire establishment can lag behind land exposure by several hundreds of years if a mire initiates through terrestrialisation or paludification (Ruppel et al., 2013; Tiselius et al., 2019). Consequently, a prerequisite of the mire chronosequence being applicable in a landscape is that primary mire formation has been the dominant mire initiation type. Despite possible overestimation of individual mire ages, the mire chronosequence approach provides a unique opportunity to study mire development and temporal variability in mire processes at the mire population level over temporal scales spanning thousands of years.

The accuracy of landscape and mire ages applied in this thesis is based on two data sources: shore displacement curves and the digital elevation model (DEM). All shore-level models entail some degree of uncertainty, often due to scarce or diverse data. The model by Påsse and Daniels (2015), which is applied in paper III, is empirical and based on a considerable number of field observations, and thus largely overcomes errors caused by data scarcity. The varved lake sediment-based model applied in papers I-II and IV comprise fewer data points, but it is based on lakes very close to the SMC, and thus has the major advantage of geographical accuracy.

The available DEM represents the present-day elevation, rather than past elevations of a paleo-DEM. Based on this, the shore-level model may be sensitive to morphological changes caused by post-glacial processes such as erosion and deposition, as well as crustal changes (Påsse and Daniels, 2015). As mires fill available depressions, the mire surface will be found at higher elevation than the elevation at mire initiation, regardless of land-uplift rate. This could be the case for mires formed through primary mire formation or paludification, although it is not necessarily the case for mires that form through terrestrialisation from lake shores. Seen at the scale of the whole landscape slope and relaxation rate, though, mire infilling is not likely to cause any major errors in the DEM or mire age intervals derived from it, as the rate of isostatic relaxation is much faster than peat growth rates. Differences in surface elevation caused by isostatic relaxation result in an elevation range of ~ 0-170 m over the SMC, while peat depths in most cases in the chronosequence are less than three meters (paper I).

3.6.3 Soil moisture compared to ground truth

The soil moisture index applied in this thesis (paper I-IV) is based on machine learning techniques with multiple topographically-derived terrain indices as input data, as well as ancillary environmental variables such as runoff and Quaternary deposits (Ågren et al., 2021; Lidberg et al., 2020). According to Ågren et al. (2021), the index outperforms all other currently available soil moisture indices, but it is less reliable near roads, where there are coarse sediments, and in areas with steep local topography. In our case, the loss of accuracy in such areas is not critical to the thesis outcomes, since the majority of these areas would be unavailable for mires (paper III). The soil moisture index describes current hydrological conditions, which may differ from past conditions both in terms of climate and anthropogenic influences. Over the course of mire lateral expansion in the SMC, the present-day, human-influenced landscape hydrology represents a very short period in a mire’s history. Most mires had already expanded into available areas before human activities influenced surface hydrology. Since our results strongly suggest that mire lateral expansion is restricted to areas that are currently moist or semi-moist (paper III), the effects of human modification of hydrological flow paths on our results and conclusions are likely to be very limited.

Flowering heath spotted-orchid (Swe. Jungfru Marie nycklar/fläcknycklar, *Dactylorhiza maculata*)

4. Concluding remarks

Many of the concepts presented in this thesis and its individual papers have previously been described using conceptual figures and models. However, few, if any, earlier studies have attempted to quantify these concepts over large spatial and temporal scales. It is precisely the landscape-wide, Holocene-level quantification of the catchment control on mire properties which is the novelty of my thesis, and which advances our understanding of mire development in the post-glacial landscape. Using the mire chronosequence approach, I was able to demonstrate how mire properties such as vegetation patterns (paper I), accumulation rates of peat mass, carbon and nitrogen (paper II), ability to expand laterally (paper III), as well as how mire patch distributions have arisen (paper IV) depend on the surrounding upland areas and, above all, on their slope and wetness. Alongside previous studies from the Sävar rising coastline mire chronosequence, we can now better understand how time and space have together shaped present mires in the post-glacial landscape. Further, by linking the mire properties studied to their catchments' eco-hydrological settings, and to successional processes shaping upland mineral soils, we can better understand how these hydrologically-connected areas interact.

Floating mat of peat-forming *Sphagnum* moss in a terrestrialised lake

5. Future perspectives

It has been very interesting to work on mire development at the wide spatial and temporal scales covered in this thesis. Nonetheless, there are many questions still to be answered before we can fully understand mire development in the post-glacial landscape. I have here compiled a few questions arising from this thesis, which could guide future studies of mire development and the interaction between mires and their upslope areas:

- How does mire initiation type affect mire, peat, and vegetation properties initially, and at later successional stages, if at all?
- Hydrologically-connected mires have different sources of water and nutrients than do unconnected systems. How does this influence nutrient transport across the landscape and between mires?
- Does within-mire variation in vegetation and accumulation rates depend on mire sub-catchments, if so, what is the relative importance of the sub-catchment support of nutrients to different mire parts, and nutrient flow within the mire area, in determining a mire's overall nutrient regime?
- How does disturbed catchment hydrology affect nutrient inflow to minerogenic mires and the balance between peat accumulation and decomposition rates?
- Will mires suffer from drought under a warmer future climate if the catchment area is unable to support them hydrologically?
- Plants are, to different degrees depending on species, flexible when it comes to nutrient demand and uptake. Is the stoichiometric flexibility in mire plants greater under conditions of weaker catchment support?
- What is the relative importance of peat growth and disconnection from mineral soil, and mire oligotrophication due to lower inflow of weathering products, on the observed negative correlation between peat nutrients, depth, and mire age in the SMC?

Tussocks formed around stems by a mire margin

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Popular science summary

Mires are a type of peatland found in many landscapes around the world. These astonishing ecosystems are popular sites for recreation, but they also provide many other services that are valuable to their surroundings and the climate, such as carbon uptake and storage, regulation of floods, and controls on water quality in downstream-located water bodies. Mires are also home to many species. Minerogenic mires, or fens, are specific types of peatland that cover large parts of northern Europe, Asia, and America. These mires receive water and plant nutrients from their upslope catchment areas and, as a result, they are also affected by processes in the catchment area. It is exactly these interactions between mires and their catchment areas that was the focus of my thesis. More specifically, I looked at how mire vegetation, peat accumulation, and expansion rates are affected by the catchment area and its properties. I carried out the study in northern Sweden in an area that covers a mire age range of 0-9 000 years. I was able to show that mire vegetation and accumulation of the nutrient nitrogen were enhanced by a stronger inflow of water and plant nutrients from the surroundings. Also, older mires with deeper peat layers had less productive vegetation. In contrast to this, I also found that accumulation rates of peat and carbon were higher in older mires with fewer incoming nutrients. Mires in the area expanded into the surrounding landscape at different speeds depending on how wet the surrounding mire margins were. Mires could occupy the wettest locations within 1 000-2 000 years after they formed, while it took 3 000-4 000 years before they had occupied the slightly drier areas that were still wet enough to hold a mire. The results of this thesis are important for the overall understanding of how northern mires develop over time and under the influence of the surrounding landscape. With this knowledge, we can better understand the extent of the different ecosystem services that mires provide.

Ripe cranberry (Swe. tranbär, *Vaccinium oxycoccos*)

Populärvetenskaplig sammanfattning

Myrar är en typ av våtmarker som återfinns i stora delar av världen. De här unika ekosystemen bidrar med ett flertal ekosystemtjänster som gynnar deras närområden och klimatet, så som upptag och -lagring av kol, reglering av vattenflöden genom landskapet och förbättring av vattenkvalitet nedströms. I myrar trivs även många karaktäristiska arter som bidrar till en högre biodiversitet på landskapsnivå. Minerogena myrar, eller kärr, är en speciell typ av myrar som täcker stora områden i de nordligaste delarna av Europa, Asien och Nordamerika. Vatten och näring når kärr från tillrinningsområdet som omger myren eller från grundvatten som sipprar upp från myrens botten. Processer utanför myren kan därför även påverka myrens egenskaper. I min avhandling har jag fokuserat på samverkan mellan myrar och deras tillrinningsområden. Jag undersökte hur myrars växtlighet, ackumulering av torv, kol och kväve, samt myrars förmåga att breda ut sig i landskapet påverkas av deras tillrinningsområden. Jag utförde studien i närheten av Umeå i ett område som täcker ett myråldersspann på 9000 år. Resultaten visade att myrens vegetation och ackumulering av kväve gynnades av ett kraftigare inflöde av vatten och näring från omgivningen, samtidigt som vegetationen i äldre myrar med djupare torv var mindre produktiv jämfört med yngre myrar. I motsats var ackumulering av torv och kol högre i äldre myrar med längre tillströmning av näring. Myrarna i området bredde ut sig till fastmarken olika snabbt och i varierande grad beroende på fuktigheten i den omgivande marken. Myrar kunde tillgodogöra de fuktigaste markerna inom 1000–2000 år, medan det dröjde 3000–4000 år innan myrarna bredde ut sig till något torrare områden. De här resultaten är viktiga med tanke på den övergripande förståelsen för hur nordliga myrar utvecklas över tid och under påverkan av det omgivande landskapet. Med den kunskapen kan vi bättre förstå vidden av de olika ekosystemtjänster som myrar erbjuder.

Ripe cloudberry (Swe. hjortron, *Rubus chamaemorus*) - The gold of the forest

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Mires are peatforming ecosystems that interact hydrologically and biogeochemically with the surrounding landscape. This thesis quantified catchment controls on key mire properties covering vegetation patterns, peat accumulation and expansion rates at the landscape level using a mire chronosequence spanning the Holocene. The results contribute to the understanding of high latitude mire development, and to scaling-up mire properties to the landscape level.

Betty Ehnvall received her PhD education at the Department of Forest Ecology and Management, SLU, Umeå. She has a Master of Science degree in Environmental Biology from University of Helsinki, Finland, and a Master of Science degree in Soil Science from SLU, Uppsala.

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