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## Global change and the functional diversity of cryptogams in northern biomes

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# Chapter 1

## General Introduction

### **Ecosystem functions of cryptogams in the (Sub)Arctic**

At high northern latitudes, cryptogams, viz. bryophytes and lichens, prevail, by far exceeding vascular plants in terms of biodiversity (Matveyeva & Chernov 2000) and also often in biomass (Wielgolaski *et al.* 1981). Cryptogams can be found as early colonizers under extreme conditions but are also present as a luxuriant ground layer in subarctic forests, their habitats ranging from hostile environments in the high alpine tundra and high arctic polar desert over vast tundra and forest ecosystems in milder environments to peatlands, efficiently storing carbon in peat layers (Longton 1988; Rydin & Jeglum 2006).

The omnipresence of cryptogams in the (Sub)Arctic is mirrored in their importance for ecosystem functioning. In extreme environments, cryptogams are the first to colonize rock and barren soil, preparing the ground for later invasion of less hardy cryptogam species and vascular plants. Especially lichens are known to promote mechanical and chemical weathering of the rock, the latter through their release of organic acids, thereby mobilizing nutrients (Adamo & Violante 2000). Cryptogamic crusts, frequently found in high alpine areas and polar deserts (Gold *et al.* 2001), consist of a complex mixture of free-living nitrogen (N<sub>2</sub>)-fixing cyanobacteria, crustose lichens and liverworts. The crust provides shelter, keeping moisture content high and temperatures low while N and organic carbon accumulate (Breen & Lévesque 2008), over time leading to first soil development. Later in succession, N<sub>2</sub>-fixing cyanobacteria also are found in symbiosis with larger bryophytes and lichens, such as *Hylocomium splendens*, *Peltigera* spp. and *Nephroma* spp., which together may account for 25-80% of annual N input in tundra ecosystems and 1-20% of total annual plant N uptake (Chapin & Bledsoe 1992). Especially in N-limited ecosystems such as the (Sub)Arctic (Haag 1974; Aerts *et al.* 1992; Shaver & Chapin 1995), this N-input can be of major importance.

A crucial ecosystem function is the storage of carbon, mainly by bryophytes, be it in tundra or, most importantly, in peatlands (cf. Limpens *et al.* 2008). Over centuries to millennia, mosses, specifically *Sphagnum* mosses, have accumulated peat in an area of  $346 \times 10^6$  ha (Gorham 1991). Carbon stored in these peatlands amounts to 600 Gt at northern latitudes, an amount equivalent to all CO<sub>2</sub> stored in the atmosphere (Clymo 1998). But also in arctic tundra, substantial amounts of (moss-derived) carbon are stored

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(McGuire *et al.* 2009). Moreover, the moss layer, predominantly covering the surface, insulates the underlying permafrost (Dyrness 1982; Gornall *et al.* 2007), dominant in vast areas of the Russian, Canadian and American Arctic. By now we have learned that both younger and older peat layers (Dorrepaal *et al.* 2009) as well as permafrost (Jorgenson *et al.* 2010) are responsive to climate change; the former by increased carbon mineralization through increasing temperatures and the latter by melting once mosses decrease in abundance (Kade & Walker 2008). Both processes lead to increased emission of the greenhouse gases CO<sub>2</sub> and CH<sub>4</sub> (Updegraff *et al.* 2001; Jorgenson *et al.* 2010), with likely positive feedback to climate warming.

Water retention by cryptogams constitutes another important ecosystem function. Especially *Sphagnum* in peatlands can store vast amounts of water due to both its high tissue water retention capacity and capillary rise of water between its stems (Hayward & Clymo 1982). As a result, these mosses create their own environment where only few other vascular plants and cryptogams are able to compete (cf. Heijmans *et al.* 2002; Hugonnot *et al.* 2003; Malmer *et al.* 2003). Also in tundra and subarctic forests, bryophyte-driven water storage may play an important role by modifying the hydrological regimes in soils (Beringer *et al.* 2001). In conclusion, despite their low stature bryophytes and lichens play a major role in the functioning of (sub)arctic ecosystems with important feedbacks to regional hydrology and even climate.

### **Assessing climate change impacts on plant communities in the (Sub)Arctic**

Climate change in the 21<sup>st</sup> century is expected to be most drastic in the northern hemisphere (ACIA 2005; IPCC 2007). In the light of the major ecosystem functions cryptogams fulfill in the (Sub)Arctic, it is important to know if and how their communities change as a result of climatic change. As different cryptogam taxa show different ecosystem functions (Cornelissen *et al.* 2007a), investigations at detailed taxonomic and functional levels are needed to understand the possible impact of climate change in the (Sub)Arctic. Unfortunately, studies conducted so far have mainly concentrated on vascular plants (Arft *et al.* 1999; Walker *et al.* 2006), while cryptogams have been largely neglected or were aggregated in major groups (Van Wijk *et al.* 2003; Wahren *et al.* 2005) rather than sampled at species level as done in only a few studies (Molau & Alatalo 1998; Press *et al.* 1998; Jägerbrand *et al.* 2009).

Climate change is expected to affect plant communities both directly and indirectly. Direct effects are manifested in the responses of community composition to increased temperature and changes in precipitation patterns, both as rain and snow (IPCC 2007).

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Some bryophytes are not yet, or only for brief periods, at their temperature optimum for photosynthesis (Skre & Oechel 1981) and would benefit to a certain limit from increased temperatures while others are adapted to more extreme i.e. cold environments. Thus, species of a more southerly and low-altitude distribution are expected to increase while species of a more northerly and/or high-altitude distribution might decrease, corresponding to shifts in lichen composition reported from the European temperate zone (Van Herk *et al.* 2002). Increases in rain would lead to increased soil moisture favoring bryophytes without belowground uptake structures such as *Sphagnum*, liverworts and most higher moss taxa. However, increasing evapotranspiration, caused by rising temperatures, might (partly) counteract this development. Increases in snow cover, however, might delay the onset of spring, on the other hand providing an additional water source at sites where water might otherwise be a limiting resource for cryptogam performance. Increasing temperatures might also lead to increased nutrient availability (Rustad *et al.* 2001), both factors favoring certain higher plant groups such as deciduous shrubs and graminoids (Van Wijk *et al.* 2003; Walker *et al.* 2006), and possibly also some faster-growing cryptogams, especially those with conducting tissues promoting uptake and transport of soil water and its nutrients. Where temperature increases lead to soil disturbances via permafrost thaw, ruderal species might appear, taking advantage of this disturbance. The appearance of shrubs and the greening of the Arctic in response to warming is a process well documented (Tape *et al.* 2006; Forbes *et al.* 2010). Slowly-growing cryptogams of low stature can easily be outcompeted by shrubs and other vascular plants through increased shading and litter coverage through increased leaf and litter production of vascular plants (Chapin *et al.* 1995; Cornelissen *et al.* 2001).

Several approaches to investigate climate change impacts on plant communities exist. These include mainly warming experiments, by using transparent open-top chambers (OTCs) (Marion *et al.* 1997), ground heating (Hartley *et al.* 1999) or greenhouses (Bret-Harte *et al.* 2001). These types of experiment offer good replication and reasonably standardized environmental factors among plots, yet they are on shorter temporal scales. Moreover, experimental artifacts such as temperature patterns deviating from climate change predictions (Kennedy 1995), changes in humidity, exclusion of precipitation (greenhouse), wind shelter and barriers for sexual and/or asexual reproduction cannot be excluded. Complementary approaches include recording of vegetation along natural climatic gradients (Gignac & Vitt 1990; Virtanen *et al.* 2006) which operate on larger spatial and temporal scales. However, confounding environmental factors such as changes in pH, soil moisture or underlying geology might be difficult to disentangle. Combining

these two approaches may therefore provide particularly robust insights (Callaghan *et al.* 1999; Cornelissen *et al.* 2001).

### **Traits of living cryptogams and their litters - implications for nutrient recycling and carbon storage**

Cryptogams are not only adapted to extreme temperature and moisture regimes but also to low nutrient availability (Longton 1988; Rydin & Jeglum 2006), a feature of major importance in a highly nutrient-limited system such as the Arctic where low temperatures lead to low mineralization rates (MacDonald *et al.* 1995; Lükewille & Wright 1997; Rustad *et al.* 2001). Fast nutrient uptake and large adsorption surfaces may be important adaptations to survive and compete under these harsh conditions. Cryptogams do indeed show specific adaptations to low nutrient availability as most cryptogams can take up nutrients with their whole shoot or thallus (Nash 1996; Bates 2000), partly even in the form of amino acids (Dahlman *et al.* 2004; Krab *et al.* 2008), which constitute an important N pool in arctic systems (Kielland 1995). Also, they are capable of translocation of nutrients from old dying parts to living material as a result of which nutrients can be re-used (Cornelissen *et al.* 2007a). In contrast with the extensive literature on nutrient retranslocation in vascular plants (Chapin 1980; Reich *et al.* 1992; Killingbeck 1996), retranslocation of nutrients in cryptogams has so far been explicitly shown for a few lichens and bryophytes only (Eckstein & Karlsson 1999; Kytöviita & Crittenden 2007). Whether or not species are more efficient at nutrient translocation may also have strong repercussions for litter quality and, consequently, litter decomposition (Aerts 1997), with a subsequent impact on carbon storage.

As discussed above, climate change is expected to change plant communities drastically in the (Sub)Arctic, promoting certain groups of higher plants which, in comparison to cryptogams, appear to produce relatively easily decomposable plant litter of high quality (see below). If this turns out to be a general pattern, carbon storage will not only decrease as a direct warming response of overall carbon mineralization, but at the same time indirectly, if different and more labile litter will be produced by higher plants. It is also important to investigate the role of interspecific variation in litter decomposability within each of the major taxa (i.e. lichens, bryophytes and vascular plants), which could also be an important driver of soil carbon dynamics. Numerous studies have investigated interspecific variation in vascular plant litter decomposability (Cornwell *et al.* 2008), also in the (Sub)Arctic (Questaed *et al.* 2003; Cornelissen *et al.* 2007b), while hardly any work has been done on cryptogams. The few studies that have been conducted concentrated on a few or single species only (Wetmore 1982; Rochefort *et al.* 1990; Hobbie 1996; Coxson

& Curteanu 2002) not allowing for generalizations at this point. For vascular plants we know that chemical traits, such as N, phosphorus and lignin content, determine decomposition rates (Swift *et al.* 1979; Palm & Rowland 1997). Yet so far, predictors of decomposability remain largely unknown for both bryophytes and lichens (Nakatsubo *et al.* 1997; Turetsky *et al.* 2008).

### **A classification of cryptogam functional groups based on traits and growth forms and their relation to ecosystem functions**

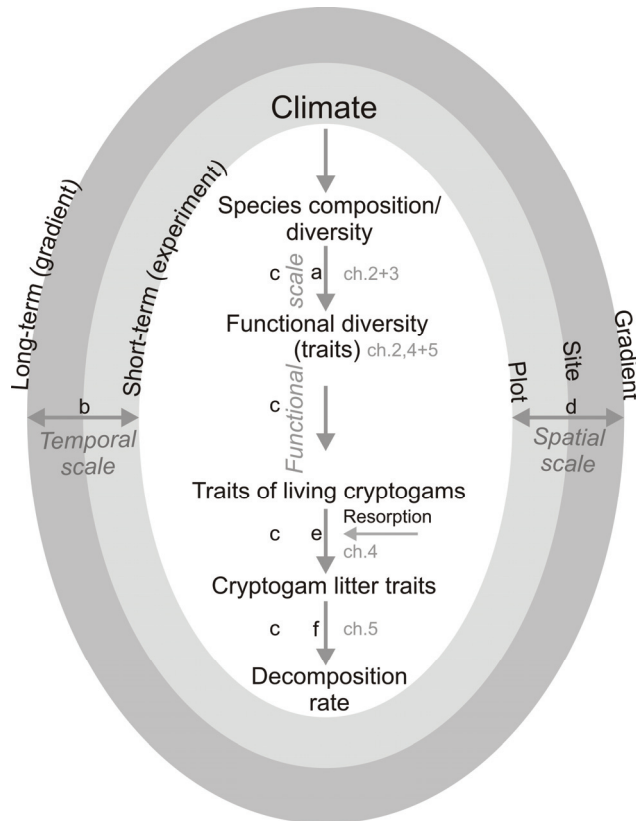
As it is impossible to study the response of each individual plant species to environmental change, many attempts have been made to classify vascular plants into functional groups based on a set of similar traits in response to environmental conditions or based on similar effects on ecosystem processes (Gitay & Noble 1997; Lavorel *et al.* 1997). In such classifications, bryophytes and lichens each have mostly been included as one functional group, with the exception of *Sphagnum* mosses whose exceptional ecosystem roles have been recognized early on (Chapin *et al.* 1996). Thus, interspecific differences within the cryptogams concerning their ecosystem functions and traits have been virtually ignored. Depending on the ecosystem processes investigated, classification criteria for functional groups may vary strongly. Obvious criteria could be the N<sub>2</sub>-fixing capacity of cryptogams where nutrient economy is concerned. Water relations might be best described by functional groups which are based on increasing degrees of water storage (cf. Smith 1988; Elumeeva *et al.* in press) and conductance efficiency of water-conducting tissues (cf. Héban 1977). Conducting tissues for transport of photosynthates, on the other hand, may play a role in nutrient resorption and translocation between cryptogam parts. A general classification of cryptogams into functional groups based on a whole set of traits, as might seem the ideal case, might therefore possibly not even serve the envisaged purpose. Rather, functional groups based on specific questions/hypotheses may be more appropriate to answer research questions as concisely as possible.

### **Aims and outline of this thesis**

This thesis investigates both the impacts of climate change on biodiversity of cryptogams in northern biomes and the consequences of these changes for some key ecosystem functions. These ecosystem functions include both the resorption of nutrients from living cryptogams during senescence and the subsequent decomposition of the remaining cryptogam litter. The impact of climate on cryptogams in the (Sub)Arctic, and its possible cascading effects on cryptogam-driven ecosystem functions through their functional traits, is illustrated in Figure 1. By investigating the influence of species composition and diversity across different temporal, spatial and functional scales, the latter from species to

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functional groups to larger taxonomical levels, the traits of cryptogams such as nutrient resorption efficiency and decomposability are studied and put into a larger context of environmental (change) drivers and ecosystem carbon and nutrient cycling.



**Fig. 1.** Climate and its influence on cryptogam diversity and its linkages, through functional traits, to nutrient resorption and litter decomposition at different temporal, spatial and functional scales.

Thus, the specific aims of this PhD study were (i) to identify the consequences of climate change for vegetation composition, specifically cryptogam composition, in the (Sub)Arctic at different temporal, spatial and functional scales and (ii) to investigate the implications of these changes concerning nutrient and carbon fluxes between the primary producers and the decomposition subsystem.

The first main aim of this study is addressed in chapters 2 and 3 (Fig. 1, relation a). Both chapters adopt the approach of combining warming manipulation experiments with natural climatic gradients. This way they study drivers of plant community composition and diversity of cryptogams and vascular plants in northern peatlands in Sweden and

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Norway, and in (sub)arctic tundra in Sweden and Alaska at different temporal, spatial and (partly) functional scales.

In chapter 2, I am specifically interested in the main drivers of cryptogam species distribution and how these drivers differ in their relative importance at different temporal (experimental, Fig.1, relation b), spatial (from micro- to macrogradient, Fig.1, relation d) and functional scales (from species level to functional group, Fig.1, relation c). Furthermore, I want to investigate whether the cryptogam species composition and diversity of these peatlands depend strongly on the development of *Sphagnum* as the underlying living substrate. Thereto, a *Sphagnum fuscum*-peatland warming experiment and its related natural climatic gradient have been investigated in subarctic northern Sweden and Norway.

In chapter 3, patterns in biodiversity and abundance changes are subsequently investigated in response to climate change in contrasting tundra ecosystems in subarctic Sweden and arctic Alaska. A wide variety of ecosystems on two continents is chosen since not only climate change is expected to vary among regions (ACIA 2005; IPCC 2007), but also ecosystems differ substantially suggesting a wide variation in ecosystem responses to climate change. Both warming experiments (Fig.1, relation b) in acidic tussock tundra in Alaska, and subarctic tundra and subarctic birch forest in Sweden, and their related natural climatic gradients (Fig.1, relation d) have been sampled. Specifically I am interested in the degree of species turnover, i.e. I hypothesize that only few bryophyte and very few lichen species are able to replace the cold-adapted species that might be lost under warmer conditions.

Chapter 4 deals with the consequences the aforesaid changes in plant community composition may have for nutrient resorption (main question 2, Fig.1, relation e). Thereto, I investigate resorption efficiencies in a wide range of cryptogams and vascular plants. Specifically, I am interested in whether the general lack or low degree of specialisation of conducting tissues in non-vascular cryptogams, as compared to that in vascular plants, has left them less efficient at nutrient resorption. I hypothesize that increasing degrees of differentiation of conducting tissues within basal cryptogam clades have led to increased resorption efficiency, and that this differentiation follows the sequence of phylogenetic branching in the Tree of Life.

In chapter 5, I compare litter quality and potential mass loss rates (decomposabilities) among a wide range of cryptogams, and a few selected vascular plants, in order to assess



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the impact changing plant communities may have on nutrient and carbon cycles (Fig.1, relation f). Both standard and novel methods to prepare and incubate cryptogam litters and to monitor their initial chemical traits are applied. These should provide us with the necessary tools to predict cryptogam litter decomposition rates across multiple species.

The concept of functional groups (Fig.1, relation c) is put to the test in chapter 2 where cryptogam growth forms depending on the biotic factor *Sphagnum* growth are developed and compared with increasingly less detailed types of classification. Also chapter 4 investigates the use of functional groups and phylogenetic positions when studying conducting tissues in cryptogams and vascular plants while chapter 5 concentrates on major taxa and the functional group of N<sub>2</sub>-fixing lichens concerning their impact on decomposition rates.

In the final chapter (chapter 6, General Discussion), I synthesize the effects of climate change onto vegetation composition in contrasting (sub)arctic ecosystems. The influence of scaling, be it spatial (along gradients), temporal (in climate change experiments) or functional (functional to taxonomical groups), on the output of the analysis is discussed. The consequences of these vegetation shifts are linked to processes such as nutrient resorption and decomposition. Furthermore, other aspects relating to cryptogam community response to climate or their subsequent impact on ecosystem function, not covered or quantified in this thesis, are highlighted. These include biotic interactions (e.g. competition, facilitation, N<sub>2</sub>-fixing capacity, herbivory), and abiotic impacts (e.g. on hydrology, permafrost insulation) related to changing plant communities.

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