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

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## Chapter 6

# General Discussion

Climate change in the (Sub)Arctic is expected to be more extreme and rapid compared to other regions in the world (IPCC 2007). Tundra and peatlands are the main ecosystem components at these northern latitudes, which are largely dominated by lichens and bryophytes fulfilling important ecosystems functions (see General Introduction, Longton 1988; Rydin & Jeglum 2006). As both biodiversity and vegetation cover in the High North are strongly determined by cryptogams (Wielgolaski *et al.* 1981; Matveyeva & Chernov 2000), investigations of changes of these indices under climate warming are of major importance. These changes in turn may have important repercussions for nutrient recycling. Therefore, the major aims of this thesis were (i) to identify the consequences of climate change for vegetation composition, specifically cryptogam composition, in the (Sub)Arctic at various temporal, spatial and functional scales and (ii) to investigate the implications of these changes concerning nutrient recycling via resorption and decomposition. Below I will discuss whether and to what extent the results presented in this thesis have fulfilled these aims.

### **Abundance and biodiversity changes in the (Sub)Arctic under climate change**

The first aim of this thesis was investigated by combining warming manipulation experiments with natural climatic gradients (see General Introduction, Fig.1, relations a, b, c and d). Studies concentrated on drivers of plant community composition and diversity of cryptogams and vascular plants in northern peatlands in Sweden and Norway, and in (sub)arctic tundra in Sweden and Alaska at different temporal, spatial and functional scales.

### **CLIMATE CHANGE-INDUCED DRIVERS OF PLANT COMMUNITIES IN SUBARCTIC PEATLANDS**

Studying peatlands in times of climate change is of major importance since they both store and still accumulate large amounts of carbon. The genus *Sphagnum* is of particular interest in that respect since it constitutes the dominant peat moss in today's peatlands and its role concerning carbon storage is unsurpassed (Rydin & Jeglum 2006). I found that *Sphagnum*-dominated plant communities in subarctic Sweden were relatively persistent against changes in temperature regimes. This is illustrated in chapter 2 where the

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influence of temperature on cryptogam composition in northern *Sphagnum*-dominated peatlands was only apparent across regions. Within one region, however, temperature influenced cryptogam composition only indirectly via *Sphagnum* growth which is partly temperature-dependent (chapter 2, Gunnarsson 2005). Moisture, while being an important determinant of *Sphagnum* growth (Gunnarsson 2005), might be less a limiting factor for this genus than for other cryptogams since *Sphagnum* displays an interesting adaptation to fluctuations in water regimes. Between stems of *Sphagnum*, water can rise by capillary forces and is held between those stems. This, together with the large water storage capacity in hyaline cells, enables *Sphagnum* to act like a sponge (Hayward & Clymo 1982). *Sphagnum* growth constitutes an important driver of plant community composition (chapter 2). This originates from its characteristics to build the ‘soil’ substrate while at the same time also being a living component of the cryptogam community. Some vascular plants, e.g. the carnivorous genus *Drosera*, are known to adjust their growth patterns to the growth of *Sphagnum*, always growing level with the top of the *Sphagnum* carpet (Rydin & Jeglum 2006). In chapter 2, I could show that this relation is found for a few cryptogams only, while most cryptogams were not able to keep up with *Sphagnum* growth. Thus, the greater the abundance of *Sphagnum* in peatlands, the less lichens, liverworts and non-*Sphagnum* mosses are found. The most important factor influencing peatland vegetation composition, however, was moisture. Since not only temperature but also precipitation regimes are expected to change (IPCC 2007), moisture rather than temperature might be the principal factor responsible for future vegetation shifts in peatlands. However, the range of mean annual temperature within the Abisko region comprised 2.3 °C (data not shown), which is well within the range of current climate projections for this century (IPCC 2007). Temperature increases larger than this range may after all lead to changes in peatland distribution, as was shown across regions with a temperature range of 4 °C (data not shown). Biogeographical differences in species assemblage between regions might be a factor influencing this output yet temperature remained significant even at growth form and major taxa level (chapter 2), thereby correcting for the influence of individual species, typical for a specific region. Also, at the limits of current peatland distribution, temperature may still play an important role in influencing peatland development and expansion. Where moisture is sufficient, *Sphagnum* growth is likely promoted by increasing temperatures at higher elevations possibly leading to an expansion of peatlands at these altitudes.

## TEMPERATURE AS THE MAIN DRIVER OF SPECIES COMPOSITION IN (SUB)ARCTIC TUNDRA

In tundra, temperature determined plant community composition along natural climatic gradients even at the regional scale (Swedish gradient, chapter 3). In contrast to *Sphagnum*-dominated peatlands, there is no strong biotic driver (*Sphagnum* growth) controlling vegetation composition but species depend on factors such as temperature, moisture and soil pH. However, vascular plants, promoted through climate warming, have been suggested to be responsible for cryptogam declines as indicated by Cornelissen *et al.* (2001) for lichens. In the warming experiments studied here, bryophytes other than *Sphagnum* were negatively affected by warming as were the lichens which appeared most susceptible. The relative resistance of *Sphagnum* to changes in temperature, as long as moisture is sufficient as discussed above, is also illustrated in chapter 3 where *Sphagnum* was able to survive as the only cryptogam even under severe warming conditions in greenhouses in arctic Alaskan tundra. It is well-known that growth of cryptogams depends on moisture conditions (Longton 1988). As bryophytes and lichens are poikilohydric, they depend almost entirely on external water supply as they do possess no or very simple conducting tissue to actively transport water (Héban 1977). In contrast to vascular plants with a more sophisticated system for internal water transport (the xylem), cryptogams cannot maintain metabolic activity as well as vascular plants during drought. Bryophytes, often growing in dense mats and supplied with rhizoids, in some species forming a dense tomentum, might sustain metabolic activity longer during times of drought by taking up water from the substrate and by offering a larger water holding capacity than most lichens. Lichens, on the other hand, grow in loose structures and often lack rhizines which intimately connect them to the ground (Smith 1988). As during the coming decades, precipitation regimes are expected to change both during winter and summer (IPCC 2007), moisture might, more than temperature, be the factor determining cryptogam performance. This may hold to a lesser extent for *Sphagnum* as this genus shows a high water holding capacity (see above), probably allowing for its high plasticity as shown in chapters 2 and 3. This water holding capacity is unsurpassed by other cryptogams which might therefore be disadvantaged in times of drought. Indeed, lichens followed by non-*Sphagnum* mosses were the first groups to be affected negatively in climate warming experiments (chapter 3). The loss of cryptogam diversity with warming and the related preferential growth of shrubs under these conditions (chapter 3), are processes taking place already now (Tape *et al.* 2006; Forbes *et al.* 2010). It has been suggested that the deposition of litter on the cryptogam layer by vascular plants, the production of which is promoted through climate warming, might accelerate the disappearance of cryptogams (Chapin *et al.* 1995). However, gradient analysis (chapter 3) showed that, depending on

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ecosystem type and bryophyte group, bryophyte abundance was either positively or negatively related to vascular plant abundance or showed no significant relation. Some bryophytes are therefore well-adapted to increasing cover and litter production by vascular plants. Lichen abundance and biomass, however, were always negatively related to vascular plant abundance and biomass, respectively (chapter 3, Cornelissen *et al.* 2001). Also, many cryptogams show a wide range of temperatures where rates of photosynthesis are still comparatively high (Tenhunen *et al.* 1992). However, growth rates of many cold-adapted cryptogam species cannot compete with those of vascular plants. As a result of a combination of the above-mentioned factors, we might have to face severe losses in diversity while cold-adapted cryptogams move further up North or to higher elevations to find refuges still suitable for their existence.

### **The influence of spatial and temporal scales in climate change investigations**

The influence of scaling importantly influenced the analyses both when working along natural climatic gradients and within experiments (see General Introduction, Fig.1, relation b and d). Whether climate warming will be important for vegetation composition and diversity, might depend on the spatial scale at which a study is conducted but also depends on the type of ecosystem, i.e. peatland (chapter 2) versus tundra (chapter 3) investigated in this thesis. Within an established ecosystem, in its optimum range, changes based on temperature regimes might not be apparent as was shown in chapter 2, where peatlands within one region were not significantly influenced by temperature. At the limits of plant distribution, however, e.g. at the limit of current peatland distribution, most future changes might be visible, with peatlands likely expanding towards higher elevations. Also within the subarctic birch forest, experimental warming had almost no effect on plant community composition (chapter 3). Above the treeline in tundra, however, warming induced a loss of cryptogam species while shrubs gained in abundance. Even though conducted at a small spatial scale, the tundra ecosystem in subarctic Sweden was clearly affected by temperature. However, the range of mean annual temperature in the studied peatlands in the Abisko region was 2.3 °C (see above) while it was 4.8 °C in subarctic Swedish tundra and 4.1 °C in arctic Alaska (data not shown). Thus, even though conducted at a smaller spatial scale, the temperature range in Swedish tundra was clearly higher, comparable to the peatland macrogradient with a temperature range of 4 °C (see above), also there significantly influencing vegetation composition.

The influence of temporal scales was most apparent in the peatland experiment conducted at a short time scale. No changes were as yet apparent (chapter 2) while long-term

investigations (9 – 16 yrs) in (sub)arctic tundra (chapter 3) clearly influenced vegetation composition. The 13-yr old experiment in the subarctic forest, however, was likely not hampered by short experimental duration but by its relative resistance to temperature changes.

Since scaling, be it spatial or temporal, importantly influenced the analyses, climate change studies should consider and evaluate their results accordingly. Short-term experiments, especially when dealing with the slowly-growing cryptogams, are unlikely to reveal any significant responses yet. Spatial scales, if comprising a larger temperature range of around 4 °C are more likely to display significant responses in vegetation composition. This temperature range is close to the mean temperature responses predicted in climate change projections for this century (ACIA 2005; IPCC 2007).

### **Cryptogam functional groups and their usage in climate change investigations**

The concept of functional groups (functional scale) has been widely used to simplify and generalize responses of species groups to environmental conditions or to describe their effects on ecosystem processes (Gitay & Noble 1997; Lavorel *et al.* 1997). Where strong biotic drivers exist, e.g. in peatlands where *Sphagnum* growth forces its own growth pattern onto other plants and cryptogams, a functional classification based on this driver was an obvious solution (chapter 2; see General Introduction, Fig.1, relation c). Along the microgradient, from plots overgrown with lichens to wet plots, *Sphagnum* growth increases and only few species are able to keep pace with the constantly growing living soil surface. Other investigations demand different classifications, e.g. based on the existence and increasing specialization of conducting tissue, when resorption efficiencies among species and species groups are compared (chapter 4). Here, taxonomic ranking was the most useful since species are grouped in genera and orders, which show the highest morphological and evolutionary similarities. Ecological functions such as the N<sub>2</sub>-fixing capacity cannot clarify the patterns in this case, since transport mechanisms of nitrogen (N) and phosphorus do not differ based on this ecosystem function. Decomposition, on the other hand, might be influenced by N<sub>2</sub>-fixation since N levels in senesced tissue are positively related to mass loss rates in cryptogams (chapter 5) and vascular plants (Palm & Rowland 1997). This does not necessarily lead to a clear distinction of decomposition rates between N<sub>2</sub>-fixing and non-N<sub>2</sub>-fixing lichens, which were indeed not different from each other in this study. On the other hand, a broad taxonomical distinction of the bryophytes into *Sphagnum*, non-*Sphagnum* mosses and liverworts helped to emphasize once more the extraordinary position of *Sphagnum* also when considering mass loss rates.

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As yet, we do not have the means to assemble a whole set of similar traits of cryptogams in response to environmental conditions or to group similar effects on ecosystem processes. If this were possible, an objective assessment of the usage of functional cryptogam groups in climate changes studies could be conducted. Until then, the use of functional or taxonomical groups based on a specific research question might be a better approach, if not the only feasible one.

### **Nutrient resorption in times of climate change**

The observed changes in plant community composition from cryptogam-dominated to shrub-dominated tundra, induced by climate change, will also affect processes related to ecosystem nutrient recycling, such as nutrient resorption from senescing tissues and litter decomposition (second aim; see General Introduction, Fig.1, relations c and e). Resorption, the translocation of nutrients from senescing plant parts into roots, stems or fresh tissue, is a process well-known from vascular plants (Chapin 1980; Reich *et al.* 1992; Killingbeck 1996). Cryptogams, however, have hardly been investigated so far (Eckstein & Karlsson 1999; Kytöviita & Crittenden 2007), despite their overwhelming contribution in terms of biomass and abundance in the (Sub)Arctic (Wielgolaski *et al.* 1981; Matveyeva & Chernov 2000). Monitoring nitrogen resorption efficiencies (RE) in a wide range of bryophytes and lichens showed that these were in general lower compared to vascular plants (except lycophytes and liverworts, chapter 4). The evolutionary appearance and increasing specialisation of conducting tissue seemed to relate to increasing levels of RE, also when observed within clades (mosses): from low RE of *Sphagnum* with almost no conducting tissue (Ligrone & Duckett 1998) to highest RE for the Polytrichales (Héban 1977; Ligrone *et al.* 2000) with a relatively high degree of specialisation in conducting tissues. High RE in vascular plants could be interpreted as an increased ability to efficiently use nutrients in a highly nutrient-limited environment. However, even though cryptogams show overall lower RE, also N levels in their tissues are lower overall (chapter 4), while in vascular plants higher RE is needed to efficiently re-use nutrients to account for the more cost-intensive vascular plant tissue (note that discrepancies in N levels between chapters 4 [high N levels of vascular plants] and 5 [N levels of vascular plants comparable to those of cryptogams] are likely based on interannual variation and the exclusion of N<sub>2</sub>-fixers and hemiparasites in the vascular plant dataset in chapter 5). Furthermore, the long lifespan and low nutrient requirements of slow-growing shoots or thalli of many cryptogam species may lead to lower levels of RE, comparable to a reduction of RE in evergreens (Aerts 1995). Long lifespan is a complementary adaptation to conserve nutrients. In conclusion, both vascular plants and cryptogams pursue different strategies to conserve nutrients, which is especially important

in a highly nutrient-limited environment such as the (Sub)Arctic (Arft *et al.* 1999). Interestingly, *Sphagnum*, with almost no conducting tissue (Ligrone & Duckett 1998) and the lowest RE, seems to compensate for this deficiency by showing an extremely high cation exchange capacity and large adsorption surfaces effectively capturing nutrients from the soil solution (Clymo 1963). As different taxa show different N levels in fresh tissues and different levels of RE, this will lead to differences in N litter concentrations. Especially *Salix* spp. and *Betula nana*, the main shrubs responsible for shrub expansion in the (Sub)Arctic, display low N levels in litter, comparable to that in cryptogams (chapter 5). Intermediate N values for these species, however, as found in the dataset underlying Quasted *et al.* (2003) used in chapter 4, are likely due to interannual variation. The shift from cryptogam- to shrub-dominated tundra will therefore result in faster internal nutrient recycling (chapter 4) but not necessarily in production of litter with higher N levels. But whether or not any such differences in litter N concentration will lead to differences in their decomposability, will also depend greatly on the structural and mobile defence chemistry of these litters, as will be discussed below.

### **Decomposition and climate change**

After resorption has taken place, leaves (or thalli) are either shed by vascular plants or remain attached to the living parts of the cryptogam while decomposition processes are initiated (see General Introduction, Fig.1, relations c and f). Clear differences can be seen in mass loss rates of the different litters that vascular plants and cryptogams produce (see Bokhorst *et al.* 2007 for an antarctic analogue, albeit with fewer species). Even though litter of vascular plants is not always richer in N than that of bryophytes, mass loss rates of vascular plants are generally higher than those of bryophytes. It is likely that in bryophytes, especially liverworts, a higher percentage of N is used in mobile secondary (defence) compounds (Asakawa 2004), which are not easily digested by the soil fauna or processed by microbes, and which are not withdrawn during the resorption process. Lichens, with high decomposition rates, are only dominant in a few places, while bryophytes are very abundant in many tundra ecosystems. Thus, a decline of bryophytes and an increase in vascular plants will lead to a much faster turnover of nutrients while the slow but continuous organic layer, built up by bryophytes over thousands of years, will cease to increase. In addition, increasing temperatures may accelerate litter decomposition (Cornelissen *et al.* 2007). While there were clear overall differences among vascular plants, bryophytes and lichens, taxonomic identity within cryptogam groups was an important determinant of mass loss rates, too. Especially *Sphagnum*, known for its recalcitrant litter (Hobbie 1996; Scheffer *et al.* 2001), showed the lowest mass loss rates within the bryophytes, and thereby contributes disproportionately to organic matter build-



up in peatlands. Within lichens, especially the Cladoniaceae showed lower decomposition rates. Locally, this might mean that mass loss rates might vary significantly depending on ecosystem type and the species present therein. These substantial interspecific differences in mass loss rates underpin the need for detailed knowledge of species identity when predicting ecosystem responses to climate change. To complicate the pattern, species do not necessarily decompose uniformly in contrasting environments (chapter 5). Therefore, there is still a great need of investigations dealing with cryptogam mass loss rates in various environments. The chemical traits determining mass loss could clearly be described by both standard wet-chemical analyses and FTIR-ATR. The advantages of FTIR-ATR as a novel method to determine primary and secondary chemistry can be seen in its efficiency and its possibility of measuring even very small samples. This is especially important when dealing with the often light-weight cryptogams where standard wet-chemical methods would be strongly disadvantaged. While many variables determining mass loss could be identified (chapter 5, Turetsky *et al.* 2008; Hájek *et al.* online), the influence of the complex secondary chemistry on decomposition still needs to be investigated further. It is likely that these chemical compounds are responsible for the differences in decomposition found in various environments. Soil microbes may be adapted to certain secondary compounds by using them as an energy source (Stark & Hyvärinen 2003). Future studies should therefore concentrate on how fast these communities can adapt to changing environmental conditions, both in terms of temperature and moisture regimes but also in terms of shifting plant communities and their related litters.

### **Outlook and conclusions**

While important effects of climate change on vegetation composition and, thereby, on nutrient recycling have been investigated in this thesis, various other aspects were not covered explicitly, such as feedback from decomposition back to carbon in the atmosphere, with possible effects on global climate itself (Wookey *et al.* 2009). It has been shown that primarily temperature and subsequent shifts in growth form composition (through leaf trait afterlife effects) affect decomposition, while differences in litter quality within species had very little effect (Cornelissen *et al.* 2007). Recalcitrant litter of shrubs, promoted by increasing temperatures (Tape *et al.* 2006), might even constitute a negative feedback to climate warming (Cornelissen *et al.* 2007). However, litter of cryptogams was hardly considered in that study. It seems likely that with the disappearance of cryptogams and their more recalcitrant litters (especially bryophytes), the overall feedback of climate warming onto decomposition might be context-dependent. In *Sphagnum*-dominated systems, the combination of strong resistance to climate change and low decomposability

together would result in carbon sequestration; in certain ecosystems dominated by non-*Sphagnum* mosses the strong decline of mosses would possibly promote carbon turnover. However, this needs to be investigated in future studies. Furthermore, herbivory by muskoxen and caribou might counteract the observed increase in shrubs as was found in a five-year study where warmed plots did not differ from control plots if grazed, while ungrazed but warmed plots shifted from graminoid-dominated toward dwarf birch-dominated (Post & Pedersen 2008). Also, direct climate effects on phenotypic expression of traits of a given species should be investigated further. Reproductive capacity and dispersal of cryptogams may be important determinants of species establishing in new regions where the climate has become or will become benign to them. Perhaps even evolution, generally leading to adaptation to climate change on longer time scales, might be of interest also at intermediate time scales of up to a century. Both topics would be relevant for further in-depth studies. While I studied chronic warming effects on vegetation composition, the influence of extreme winter warming events, possibly leading to shifts in plant communities, should be extended to cryptogams (cf. Bokhorst *et al.* 2008 for vascular plants). Biotic interactions such as competition and facilitation, between vascular plants and cryptogams as well as within cryptogams, might cause shifts in species biomass distributions. We still know very little about how such shifts would affect abundance-weighted processes like decomposition rates (cf. Fortunel *et al.* 2009 for vascular plants). Furthermore, N<sub>2</sub>-fixation capacity in cryptogams (Gavazov *et al.* 2010) and how this capacity is influenced by changes in vegetation composition could be of interest in future climate change investigations. Other important aspects (abiotic interactions) not treated here include the effects of changing vegetation composition onto permafrost insulation (Gornall *et al.* 2007). As bryophytes disappear, the active layer will increase (Kade & Walker 2008), releasing larger amounts of the greenhouse gases CO<sub>2</sub> and CH<sub>4</sub> into the atmosphere (Jorgenson *et al.* 2010). Also hydrology, strongly influenced by bryophytes (Beringer *et al.* 2001; Heijmans *et al.* 2004) would be worthwhile investigating. My study focussed on vegetation shifts induced by climate change and its implications for nutrient resorption and decomposition. The most drastic changes in vegetation will likely be visible at the individual limits of the species' ecological optimum range, i.e. at community level at or above treeline, or might be seen at species level for instance in the expansion of peatlands through *Sphagnum*. What is needed in future climate change studies is a linkage between climate change studies and ecosystem traits as mentioned above, which need to be quantified in order to be able to predict effects of climate change onto ecosystem functioning in the (Sub)Arctic. Specifically, interspecific differences in these ecosystem traits might be the key to a deeper understanding of the complex relationships determining the nutrient, carbon and water dynamics of the

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(Sub)Arctic and their response in times of climate change. In that sense this thesis, in spite of the complexity of the above mentioned (and further) interacting factors, has added significantly to finding this key. Indeed, it has revealed important new information towards fulfilling the two main aims of this thesis by (i) identifying the likely consequences of climate change for specifically the cryptogam component of vegetation composition in the (Sub)Arctic at various temporal, spatial and functional scales and by (ii) demonstrating the likely implications of these changes for nutrient recycling via nutrient resorption and litter decomposition.

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