

# Effects of climate change on boreal wetland and riparian vegetation

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Cover: *Carex acuta* and *Calamagrostis canescens* in Strycksele, by Lotta Ström

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*Till Gunnar och Britta*

## List of papers

This thesis is a summary of the following papers that are referred to in the text by their Roman numerals:

- I. Ström L., Jansson R., Nilsson C., Johansson M. E. & Xiong S. J. (2011)  
**Hydrologic effects on riparian vegetation in a boreal river: an experiment testing climate change predictions**  
*Global Change Biology*, **17**, 254-267.
- II. Ström L., Jansson R. & Nilsson C.  
**Projected changes in plant species richness and extent of riparian ecosystems as a result of climate-driven hydrologic change**  
Submitted manuscript.
- III. Ström L., Jansson R. & Nilsson C.  
**Projected changes in hydrologic niches of riparian plants in response to climate change**  
Manuscript.
- IV. Ström L., Jansson R. & Nilsson C.  
**Differences in plant invasibility among boreal wetland communities**  
Submitted manuscript.

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# Abstract

Models of climate change predict that temperature will increase during the 21<sup>st</sup> century and the largest warming will take place at high northern latitudes. In addition to warming, predictions for northern Europe include increased annual precipitation and a higher proportion of the precipitation during winter falling as rain instead of snow. These changes will substantially alter the hydrology of rivers and streams and change the conditions for riverine communities. The warming is also expected to result in species adjusting their geographic ranges to stay within their climatic tolerances. Riparian zones and wetlands are areas where excess water determines the community composition. It is therefore likely that these systems will be highly responsive to alterations in precipitation and temperature patterns.

In this thesis we have tested the predicted responses of riparian vegetation to climate-driven hydrologic change with a six year long transplant experiment (I). Turfs of vegetation were moved to a new elevation with shorter or longer flood durations. The results demonstrate that riparian species will respond to hydrologic changes, and that without rare events such as unusually large floods or droughts, full adjustment to the new hydrological regime may take at least 10 years.

Moreover, we quantified potential effects of a changed hydrology on riparian plant species richness (II) and individual species responses (III) under different climate scenarios along the Vindel River in northern Sweden. Despite relatively small changes in hydrology, the results imply that many species will become less frequent than today, with stochastic extinctions along some reaches. Climate change may threaten riparian vegetation along some of the last pristine or near-natural river ecosystems in Europe. More extensive loss of species than predicted for the Vindel River is expected along rivers in the southern boreal zone, where snow-melt fed hydrographs are expected to be largely replaced by rain-fed ones.

With a seed sowing experiment, we tested the differences in invasibility between open wetlands, forested wetlands and riparian zones (IV). All six species introduced were able to germinate and survive in all habitats and disturbance levels, indicating that the tested wetlands are generally invulnerable. Germination was highest in open wetlands and riparian zones. Increasing seed sowing density increased invasion success, but the disturbance treatments had little effect. The fact that seeds germinated and survived for 2 to 3 years in all wetland habitats indicates that wetland species with sufficiently high dispersal capacity and propagule pressure would be able to germinate and establish here in their respective wetland type. Our results clearly demonstrate that a changed climate will result in substantial changes to functioning, structure and diversity of boreal wetland and riparian ecosystems. To preserve species rich habitats still unaffected by dams and other human stressors, additional protection and management actions may have to be considered.

**Keywords:** biomass, flooding, hydrologic niche, invasibility, riparian zone, riparian plant species, river margin, climate scenario, seed sowing experiment, species composition, species richness, transplant experiment

# Introduction

Global mean annual temperature has increased by 0.7°C during the 20<sup>th</sup> century (IPCC 2007) and models of climate change predict that temperature will continue to increase. The largest warming will take place at high northern latitudes (IPCC 2007), a fact that makes studies of northern ecosystems and their response to climate change highly important. In addition to warming, predictions for northern Europe include increased annual precipitation and a higher proportion of precipitation falling as rain instead of snow during winter (IPCC 2007). These changes will substantially alter the hydrology of rivers and streams (Andréasson *et al.* 2004; Woo *et al.* 2008). Annual stream flow in rivers at high northern latitudes has already increased in recent decades in concurrence with warming of the climate (Peterson *et al.* 2002), findings that support projections for the future.

Riparian zones and wetlands are areas where excess water determines the community composition (Keddy 2000). It is therefore likely that these systems will be highly responsive to alterations in precipitation and temperature patterns.

## **Changes in river-flow**

The seasonal timing and amount of flow variation vary with latitude, degree of climate continentality, topography and influence of buffering waterbodies, and thus the response to climate change will vary among rivers and regions (Woo *et al.* 2008). Stream-flow regimes in the boreal zone are strongly seasonally variable. In natural conditions they are characterized by a spring flood with the annual peak water-level caused by snowmelt. The spring flood is then followed by decreasing discharge during summer and autumn (Woo *et al.* 2008), with occasional summer and autumn flood peaks caused by rain. During winter the flow is low and primarily fed by groundwater discharge. Earlier snowmelt and thinner snow packs will result in earlier spring floods of lower amplitude (Andréasson *et al.* 2004; Woo *et al.* 2008). Hydrologic models for Sweden predict mean annual runoff to increase by up to 24% in the boreal part with decreased spring flood peaks, increased frequency of high flow events during autumns, and higher winter flows (Andréasson *et al.* 2004). Not all high-latitude river systems are expected to change hydrologically: in the Arctic, prolonged periods with below-zero temperatures will still occur and increased precipitation might even lead to deeper snow packs. Hence, spring flood peaks are likely to be preserved (Dankers & Middelkoop 2008).

## **Flow regime and vegetation**

Riparian communities are controlled by magnitude and variation in stream flow (Décamps 1993; Naiman & Décamps 1997; Poff *et al.* 1997). If aspects of flow are changed, this is expected to have consequences for the frequency and abundance of species, as well as for their dispersal capacity (Nilsson *et al.* 2010). Plant species in riparian zones are structured by differences in the hydrologic niche, with strong trade-offs between adaptations to drought tolerance and aeration during submergence (Silvertown *et al.* 1999). They vary in their tolerance to inundation (Vervuren, Blom & Kroon 2003; Glenz *et al.* 2008), with important intraspecific variation among populations (DeCarvalho *et al.* 2008) or between sexes (Hughes *et al.* 2010; Nielsen *et al.* 2010). The vegetation is especially sensitive to changes in minimum and maximum flows, and substantial changes may take place without a change in mean annual flow (Auble, Friedman & Scott 1994). Floods pose stress to riparian plants by negatively affecting physiological processes such as photosynthesis and respiration (Kozlowski 1984; Vervuren *et al.* 2003; van Eck *et al.* 2004; Mommer & Visser 2005; Renöfält, Merritt & Nilsson 2007), and act as a disturbance by removing plant biomass (Bendix 1999) or burying plants under deposits of sediment or organic matter (Xiong & Nilsson 1997). Riparian plant species segregate into plant communities with different plant traits depending on flood disturbance intensity (Bornette *et al.* 2008). Flood disturbance may enhance species richness by suppressing dominants and enhancing the colonization and survival of competitively subordinate species (Day *et al.* 1988; Pollock, Naiman & Hanley 1998). However, stress and disturbance may also exceed the tolerance of species, creating a unimodal relationship between plant species richness and flood magnitude or frequency (Pollock *et al.* 1998).

## **Wetlands and riparian zones**

Riparian zones are by definition wetlands, but they are often treated separately in the literature. This is mainly because different types of processes are responsible for structuring functioning and diversity in these systems. Wetland types and riparian zones vary in their ecological characteristics depending on differences in disturbance, nutrient load, and water-level fluctuations (Keddy 2000). Wetlands are more stable compared with the frequently disturbed riparian areas. In the forested wetlands flood events are short and mostly associated with snow melt, whereas the open wetlands may be more or less permanently submerged, although mean depth is low (Keddy 2000). In the riparian zones, plants have to cope with periods of both inundation and drought, primarily resulting from spring floods associated with snowmelt followed by decreasing water-levels (Nilsson *et al.* 1993). The riparian zones are also characterized by disturbance from flowing water, resulting in erosion and redistribution of sediment and organic matter

(Nilsson 1999). Many species can grow in all three of these habitats, but species richness is highest in the riparian zones (Nilsson 1999).

Wetland types and riparian zones also differ significantly in their spatial distribution. Riparian zones cover only small proportions of the land area but are highly connected across landscapes owing to their linear shape and the high connectivity of stream networks (Ward & Stanford 1995; Wiens 2002). In contrast, wetlands cover larger areas but primarily occur as patches within a matrix of dry to mesic coniferous forests. In the boreal region wetlands are common and diverse, making up significant proportions of boreal landscapes. Eleven percent of Sweden's total area, or 4.9 million ha, consists of natural and semi-natural mires (Rydin *et al.* 1999).

### **Species migrations**

Global climate change is expected to result in species adjusting their geographic ranges to stay within their climatic tolerances (Walther *et al.* 2002; Parmesan & Yohe 2003; Thuiller *et al.* 2005). Range adjustments imply establishment of populations beyond the current geographical range limit and makes invasion ecology highly relevant in predicting responses to climate change. The potential for range adjustments will depend on the spatial configuration of ecosystems in landscapes (Engler & Guisan 2009; Wilson *et al.* 2010). Both natural and human-dominated landscapes are often fragmented, with barriers against dispersal of species inhabiting isolated or disconnected ecosystems

Three factors have been suggested to influence invasion success: the number of propagules of an invading species, the characteristics of the invading species or its *invasiveness*, and the *invasibility* of the new environment (Lonsdale 1999). Propagule pressure, measured as the number of individuals and introduction events, is generally considered to explain much of the variation in plant invasion success (Lockwood 2005; von Holle & Simberloff 2005; Colautti *et al.* 2006). Plant traits resulting in high invasiveness depend strongly on the environment being invaded (Tilman 1997; Thompson *et al.* 2001; von Holle 2005). However, traits like large seed size and germination characteristics are generally important at initial stages (Burke & Grime 1996), and more generally traits associated with *r* strategists are correlated with invasive spread (Rejmanek & Richardson 1996; Grotkopp *et al.* 2002; Sutherland 2004). Successful invaders have been reported as often being functionally similar to native species (Thompson *et al.* 1995; Rejmanek & Richardson 1996), reflecting the importance of local environmental conditions.

Invasibility is the susceptibility of an environment to colonisation and establishment of individuals from species which are currently not part of the resident community (Davis *et al.* 2005). It is a function of both the abiotic and biotic environments (Catford *et al.* 2009), but has mostly been

considered in relation to community diversity (Roscher *et al.* 2009). Positive or negative correlations are considered a matter of scale with negative effects of diversity on invasibility primarily observed at small spatial scales where neighbouring plants directly interact (Levine & D'Antonio 1999). In contrast, at larger spatial scales correlations between native and exotic diversity are mostly positive, and can be explained by native and invading species responding similarly to the local environment (Davis *et al.* 2000; Brown & Peet 2003). Thus, invasibility can be controlled by fluctuating resources (Davis *et al.* 2005), soil fertility (Leishman & Thomson 2005) or the interaction between disturbance and fertility (Burke & Grime 1996), with high establishment success in turn promoting diversity (Davis *et al.* 2005).

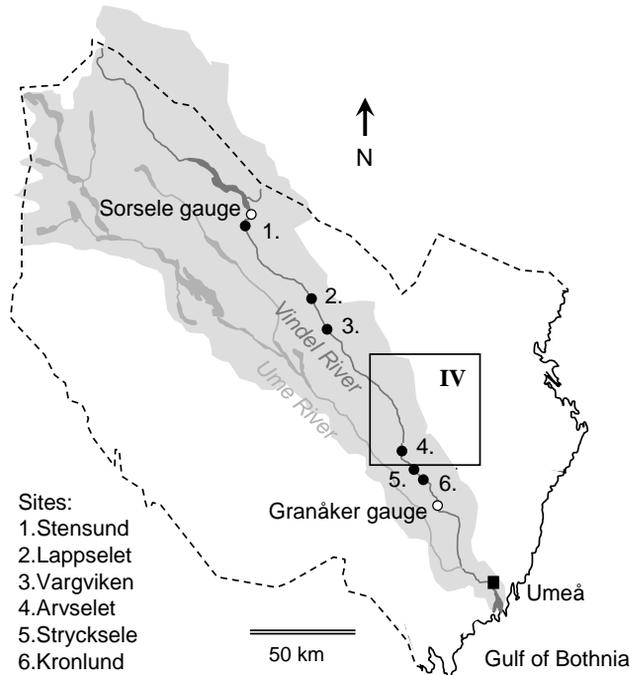
## Aims

In this thesis we studied the relationship between riparian vegetation and flooding along the main channel of a seventh order river (**I**, **II**, **IV**). We also compared the invasibility of the three categories of wetland (**IV**): riparian zones along smaller streams, open wetlands and forested wetlands (Fig. 1, **IV**). The overall aim was to test predicted responses of riparian vegetation to climate change. Moreover, we wanted to quantify potential effects of a changing climate on wetland communities and on riparian vegetation under different climate scenarios. The main questions asked are:

- Will changes in flood duration and frequency affect the richness and species composition of riparian plant communities and alter biomass production? **I**
- How will projected future hydrologic regimes affect the areal extent of riparian zones and the species richness of riparian species? **II**
- How will individual plant species in riparian zones respond to climate driven hydrologic changes? **III**
- Is there a difference in invasibility between different kinds of wetlands? **IV**

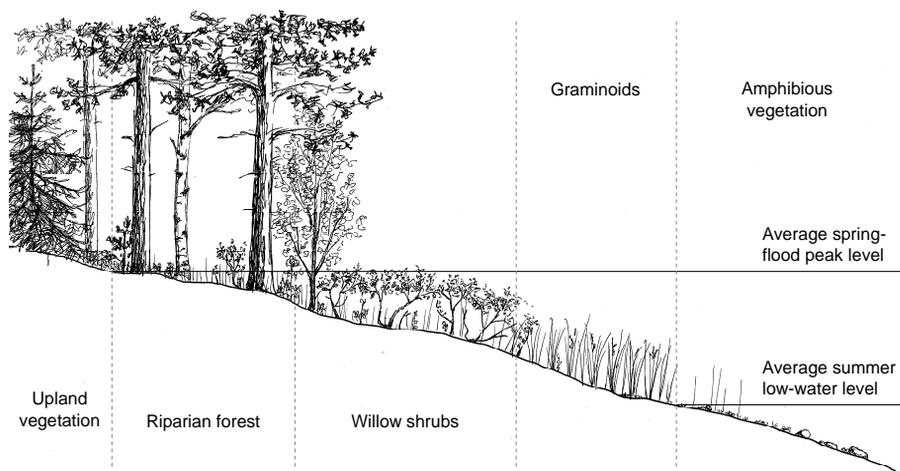
## Study area

Three of the studies in this thesis (**I**, **II**, **III**) were carried out along the free flowing Vindel River in Northern Sweden (Fig. 1). The 455 km long river originates in the Scandinavian mountain range and joins the Ume River about 40 km upstream from the Gulf of Bothnia. Mean annual discharge at the confluence is 200 m<sup>3</sup>/s and annual minimum and maximum flows varied between 16 and 1787 m<sup>3</sup>/s during 1911–2000 (data from the Swedish Meteorological and Hydrological Institute [SMHI], Norrköping, Sweden). The hydrologic regime is characterized by a spring flood peak due to snowmelt in May or June followed by progressively lower water levels during summer and winter. In some years summer and autumn rains and reduced evapotranspiration towards the end of the growing season result in additional flood events. The Vindel River alternates between stretches of rapids and tranquil reaches along its entire course. There are two gauges in the river: Granåker is located in the lower part and Sorsele higher up in the system (Fig. 1).



**Fig. 1.** The Ume river catchment with the sites used in the thesis. The square marks the area used in paper IV.

The river-margin vegetation is distinctly vertically zoned along the entire river. Down an elevation gradient, plant cover changes from riparian forest through zones of riparian shrubs and graminoids to amphibious plant communities (Fig. 2). Trees in the riparian forest are dominated by Scots pine (*Pinus sylvestris* L.), grey alder (*Alnus incana* (L.) Moench) and downy birch (*Betula pubescens* Ehrh). The riparian shrubs mainly consist of willows (*Salix* spp.), while sedge (*Carex* spp.) are most abundant in the graminoid zone. The amphibious vegetation is dominated by small rosette plants tolerant of extended periods of submergence such as *Ranunculus reptans* L. and *Subularia aquatica* L. The limits and widths of vegetation belts can be defined by hydrologic criteria, the upper end of riparian vegetation being equivalent to the spring-flood peak level, whereas the lower end of graminoid vegetation is synchronous with average summer low water-levels (Wassén, 1966; Nilsson, 1999). Understorey vegetation of adjacent uplands is dominated by species poor communities of dwarf shrubs, such as *Vaccinium myrtillus* L. and *V. vitis-idea* L.. The riparian vegetation of the catchment is primarily composed of native species; only a few occurrences of exotic species are known and invasive species are absent (Nilsson 1999, Dynesius *et al.* 2004). The average length of the annual growing season (days where the average temperature exceeds +5°C) ranged between about 125 days in the region of the most upstream site (Sorsele) to about 145 days for the region of the lowest site (Kronlund) for the period 1961–1990 (data from SMHI, Norrköping, Sweden).



**Fig. 2** A schematic drawing of a boreal riparian zone.

The experiment for paper **I** was conducted on a floodplain meadow in Strycksele, along the lower reaches of the river. Up to the 1950s and 1960s,

most riparian zones along tranquil reaches with fine-grained soils were used for haymaking, favouring plant communities rich in graminoids and forbs. Following abandonment, riparian tree and shrub species have colonized higher elevations of these meadows.

We located six study sites to tranquil reaches for paper **II** ranging from 165 to 340 m above sea level (Fig. 1). The three most upstream sites; Stensund, Lappselet and Vargviken were located above the former highest coastline marking the position of the highest post-glacial shoreline of a precursor (the Ancylus Lake) of the Baltic Sea, now situated about 250 m above the present sea level as a result of crustal rebound (Fredén 1994). The remaining three sites; Arvselet, Strycksele and Kronlund were situated below the former highest coastline. The Strycksele site is not the same as in paper **I**, but situated about 550 m further upstream. Five of the six sites were also used for paper **III**. Stensund was excluded since it was the only site with a flow-regime that corresponded better with the gauge in Sorsele than Granåker.

The study for paper **IV** was located in the vicinity of Åmsele in the county of Västerbotten, Sweden, about 80 km northwest of Umeå (Fig. 1), within a 50 × 50 km large area (representing a map sheet, 22J Kalvträsk, Lantmäteriet's road map). This area was chosen for the patchy distribution of various habitat types, a result of the last glaciation when this area was the location of the highest coastline. Soils in this area are generally nutrient poor and plant species richness low, with some wetland types being the most species-rich habitats for plants (Zinko *et al.* 2005). Comparing between the wetland types, the forests have the most dense tree cover, resulting in less direct sunlight and more leaf litter in autumn. In contrast, the open wetlands have at most a sparse tree cover of mainly small individuals of Scots pine *Pinus sylvestris* L. or downy birch *Betula pubescens* Ehrh. and high insolation during the growing season. Whether or not wetlands are forested depends on the duration of water tables at or close to the soil surface, creating anaerobic conditions unsuitable for woody plants (Rydin *et al.* 1999). The riparian zones have a wide range of tree cover depending on width of the zone.

## Methods

### Vegetation

For the vegetation surveys we used three different methods. In paper **I** we recorded the frequency of all vascular plant species using a point touch method (16 points in a 50 x 50 cm area, 10 cm from the edge of the plots, to minimize edge effects) where every species touching the stick was recorded

once at each point, i.e., the maximum score was 16 per plot. In addition, the presence of any additional species in the plot was recorded. Plant biomass was harvested from subplots (15 x 20 cm) nested within each plot. After harvest, biomass was dried at 60 °C for 72 h and weighed.

In paper **II** and **III** we recorded presence of all species rooted within 50 × 50 cm large plots along with the percentage cover of vegetation (vertical projection going from 0 to 100%). Each plot was also classified to one of five vegetation belts, i.e. upland vegetation, riparian forest, willow shrub, graminoid or amphibious vegetation. The elevation of the surveyed plots was measured with a total station (an integrated electronic theodolite and distance meter) with 1 cm accuracy (Geodolite 506, Trimble Navigation Limited, Sunnyvale, CA, USA).

In paper **IV** for the germination experiment, seeds of six species were sown in separate subplots. The species represent a selection of growth forms and all belong to the flora of the region: *Betula pubescens* (deciduous tree), *Andromeda polifolia* L. (dwarf shrub), *Carex magellanica* Lam. (rhizome-forming graminoid), *Molinia caerulea* (L.) Moench (tussock-forming graminoid), *Filipendula ulmaria* (L.) Maxim. (high forb), and *Potentilla palustris* (L.) Scop. (low forb). All species are perennials. Survey of the composition of local vegetation was carried out by recording the presence of all vascular plant species in 50 × 50 cm large plots and classifying them into five cover classes: 1: ≤1%; 2: 2–10%; 3: 11–25%; 4: 26–50%, and 5: >50%. Two plots were sampled at each site. Tree canopy cover was estimated for each plot with a spherical densiometer (model A).

The definition of a species follows the taxonomy in Krok & Almquist (1994).

## Hydrology

Soil moisture was measured both with plaster cubes in the ground and a soil moisture meter (Model 14.22, Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands) (**I**) and with a time domain reflectometer (Trime®-TDR, IMKO GmbH) (**III**, **IV**). Local water levels were measured with pressure transducer data loggers (Diver, van Essen Instruments Limited, Delft, the Netherlands) recording the depth of the water column on top of the logger, hanging in a well inserted into the ground (**I**, **II**, **III**).

Simulations of future streamflow were obtained from SMHI (Andréasson *et al.* 2004) (**I**, **II**, **III**). They were calculated to correspond to the period 2071–2100 at the Granåker and Sorsele gauges in the Vindel river. The Rossby Centre Regional Atmosphere–Ocean Model (RCAO) and the runoff model HBV developed by SMHI were used along with data from two general circulation models: HadAM3H from the Hadley Centre of the UK

Meteorological Office and ECHAM4/OPYC3 from the Max-Planck Institute for Meteorology in Hamburg. The general circulation models were run with data according to the A2 and B2 IPCC emission scenarios (Nakicenovic & Swart, 2000), where the A2 scenario predicts larger increases in greenhouse gas emissions than the B2 scenario (for detailed description of the simulation models, see Andréasson *et al.*, 2004).

## Summary of papers

### **I. Hydrologic effects on riparian vegetation in a boreal river: an experiment testing climate change predictions**

We evaluated ecological responses of vascular plants to climate change by transplanting turfs of riparian vegetation to new elevations in the riparian zone, thus simulating changes in water-level variation. A total of 96 plots, 70 x 100 cm in size, were distributed at three elevations, high mid and low, corresponding to the riparian belts of forest, shrub and graminoids. Excavated turfs were either transplanted to one of the other two elevations or they were rotated 180° and then put back into their original positions to evaluate the effect of excavation. The remaining fourth of the plots were left intact serving as controls. The experiment was monitored for 6 years. The overall effect was that turfs transplanted to higher elevations decreased in biomass and increased in species richness, whereas turfs transplanted to lower elevations gained in biomass but lost in species richness. At the end of the experiment, biomass was statistically different between high and low elevation and biomass in turfs transplanted between them was statistically indistinguishable from the target level. Species richness in the control plots differed between the low elevation and the other two elevations. The number of species in the transplanted turfs was either more similar to the target level or intermediate between origin and target levels. Species composition differed statistically between all elevations and the transplants were mainly intermediate in transition between original and target levels. When moved to mid elevations the composition of turfs was still most similar to the origin, but turfs moved from high to low elevations were statistically indistinguishable to the new elevation. No species other than those already growing in the meadow at the start of the experiment invaded the turfs during the 6 years.

Our experiment demonstrates that riparian-plant communities will change in response to the hydrologic alterations expected as a result of climate change. Transplanted plant communities responded slowly to the new hydrologic conditions and had not fully adjusted to the new elevation 6 years

after transplantation. Extrapolating from our results suggests that full adjustment to the new hydrological regime will take at least 10 years, but rare events such as unusually large floods or droughts may result in non-linear vegetation responses (Jentsch *et al.* 2007). Climate change is expected to occur gradually over time whereas our experimental design resulted in an instantaneous hydrologic change. However, this allowed us to estimate the actual rate of vegetation response. The long time for community adjustment required shows the importance of conducting long-term field experiments (Milchunas & Lauenroth 1995).

## **II, III. Projected changes in the extent of riparian ecosystems, plant species richness and species hydrologic niche as a result of climate-driven hydrologic change.**

We quantified effects of predicted hydrologic change on riparian vegetation, using four different scenarios for the free-flowing Vindel River in northern Sweden. At six sites, 21 transects were placed perpendicular to the riparian zone with 5 m in between. The plots were placed with 25 cm difference in elevation with approximately three plots above the average annual high water-level in upland vegetation and continued down into the river channel to a current water depth of about 40 cm, situated in the amphibious vegetation belt. In total, 1733 plots was used for paper **II**, and for paper **III**, we used five of the six sites, resulting in 1395 plots.

### ***River-flow scenarios***

Changes in elevational limits of plant species and vegetation belts were calculated by relating flood duration for each plot during 10 years preceding vegetation survey with the flood duration expected for 2071–2100. The predicted lower spring-flood peaks will reduce the riparian area from the upper elevation, potentially allowing upland species to invade (Table 1). The emission scenario A2 is based on higher release of greenhouse gases and more hydrologic changes than B2 and therefore predicts larger changes in elevation. Increases in discharge are mainly predicted for the period outside the growing season, when present levels are at its lowest (Andréasson *et al.* 2004). Plants are more sensitive to flooding while photosynthetically active, but disturbance from ice scour during winters at higher riparian elevations than today might significantly influence species occurrences. The general circulation model ECHAM4 predicts a larger increase in precipitation and therefore a larger reduction of the riparian zone from below, especially when considering duration during the entire years (Table 1). In both of the papers (**II**, **III**) we present the results from the worst case and the best case scenarios; ECHAM4 with the A2 scenario (E-A2) and HadAM3 with the B2 scenario (H-B2).

**Tab. 1** A simplified summary of predicted shifts in elevation of the riparian zone's upper and lower limits. Arrows indicate the direction of change and the relative extent. Time period = whether changes are calculated based on predicted flood durations during the growing season or the entire year. Scenarios are calculated with the two Global Circulation Models, ECHAM4 and HadAM3H, and two emission scenarios, A2 and B2

Time period	Limit	ECHAM4		HadAM3H	
		A2	B2	A2	B2
Growing season	Upper	↓	↓	↓	↓
	Lower	↑	↑	↓	↑
Year	Upper	↓	↓	↓	↓
	Lower	↑	↑	↑	↑

### ***Species richness II***

We calculated the hydrologic niche of each vegetation belt by relating the occurrence of species in the plots with the flood duration for 10 years preceding vegetation survey. We then used the flood duration predicted for 2071–2100 to estimate expected changes in the extent of each vegetation belt. Using species accumulation curves, we then predicted changes in plant species richness as a result of changes in extent.

The two most species-rich vegetation belts, the riparian forest and the willow shrub belts, were predicted to decrease most in elevational extent, up to 39% and 32% respectively. For the lower elevations changes differed between scenarios and whether flood duration during growing season or the entire year were considered. When considering duration during growing season, changes were small. When flood duration for the entire year were used the graminoid belt below the shrub belt is predicted to shift upwards in elevation while the amphibious vegetation belt at the bottom of the riparian zone would increase in size.

In the Vindel River, the riparian forest and willow shrub zone are predicted to lose most species, with reductions of 5–12% and 1–13%, respectively, depending on scenario. When we combined the riparian forest, willow shrub zone and the graminoid zone to the entire riparian zone reductions are predicted to be smaller, 1–9% or 1–8 species, since many species occur in more than one vegetation belt.

### ***Elevational extent of species III***

To estimate future changes in the occurrence of individual species in riparian zones, their probability of occurrence was calculated along the gradient of flood duration. The hydrologic niche of each species was then compared with the inundation duration corresponding to the predicted future stream-flow in the same way as for the vegetation belts.

The majority of the riparian species are predicted to decrease in elevational extent by on average 13–28 %, depending on scenario and if flood duration during growing season or the entire year is considered. Species growing in the upper, spring-flood controlled part of the riparian zone are predicted to decrease most, with largest reductions in species with narrow flood duration ranges. Examples of such species, i.e. the species expected to decrease most among the tested are: *Alnus incana*, *Andromeda polifolia* and *Valeriana sambucifolia*. They are expected to lose about 40–50 % of their extent depending on scenario, but these species are common also in other types of wetlands. *Scutellaria galericulata* and *Poa palustris* on the other hand are predicted to lose about 25–40 % and they are less common in the region and more or less restricted to riparian habitats. Aquatic species are also predicted to experience large reductions, but mainly under the H-B2 scenario. *Eleocharis acicularis* and *Alopecurus aequalis* would lose about 40 and 30% respectively. Most species would become less frequent than today, with stochastic extinctions expected along some reaches.

### ***Discussion and Conclusions***

The climate-driven hydrologic change expected until the end of the century would result in reduced elevational extents and fewer occurrences of most plant species in riparian zones. The results demonstrate that climate change may threaten some of the last pristine or near-natural river ecosystems in Europe little affected by other human stressors (Nilsson *et al.* 2005). We do not imply that any of the predicted scenarios will necessarily come true, but our results show that changes may be large despite moderate changes in flow.

The mechanism behind the larger decrease in extent of the riparian forest and the willow shrub zone, the large reductions of species niches and the higher species losses in this area is that the predicted change flood duration is steeper at this elevation than other ones. The altered flood duration implies a drier upper part, as a result of lower spring flood peaks, and a wetter lower part. Species growing there with at least one of the limits either higher up or further down are predicted to decrease less. More dramatic reductions of the riparian zone and more extensive species losses are expected along rivers in the southern boreal zone, where snow-melt fed hydrographs are expected to be largely replaced by rain-fed ones.

Although most species are predicted to become less frequent in riparian zones along the Vindel River, no species was predicted to lose more than about 50 % of its elevational extent. Nevertheless, this would likely entail that many species would become less frequent than today, with stochastic extinctions along some reaches. The projections of climate change can be compared with effects of flow regulation for hydropower production, which entailed replacing natural flow regimes with either increased frequency or changed timing of water-level fluctuations. Regulation made most riparian plant species less frequent, but resulted in few river-wide extinctions (Nilsson *et al.* 1991; Jansson *et al.* 2000). However, regulation caused species in the regulated Ume River to disappear from a third of the sites (Nilsson *et al.* 1991), but we predict few extinctions from each site. On the other hand, some plant species might disappear as a result of combinations of changes in hydrology, climate and biotic interactions. At present only a few occurrences of exotic species are known in the Vindel River catchment and invasive species are absent (Nilsson 1999, Dynesius *et al.* 2004). We only considered changes in flood duration, but other changes associated with climate change, such as increased temperatures and ice scour at higher elevations in riparian zones might benefit the invasion of new species.

With few rivers remaining unaffected by dams and other human stressors, even moderate reductions in abundance can have grave consequences for regional conservation. If enhanced protection of free-flowing streams is not sufficient to preserve the species-rich riparian streams in their current state, monitoring to detect declining species and additional management to minimize species losses have to be considered. Management might include protection of more riverine ecosystems, reduction of negative impacts from land-use activities, implementation of more environmentally friendly flows, channel restoration, and more artificial management options such as mowing riparian meadows no longer maintained by recurrent floods.

#### **IV. Differences in plant invasibility among boreal wetland communities**

We made a seed sowing experiment in northern Sweden to test for differences in invasibility between three major wetland types, with the seed success summarizing differences in abiotic and biotic control of germination and survival among the wetlands. In riparian zones, open wetlands and forested wetlands, six local wetland species were sown separately in plots with two different levels of disturbance and monitored for 3 years. For two species, seed sowing density was varied to test for effects of propagule pressure. All six species were able to germinate and survive in all habitats and disturbance levels. All species germinated best on the bogs or in the riparian plots. The effect of disturbance was low, only being important for

two species. Survival was also mainly explained by habitat except for one species. The frequency of germination did not vary with seed sowing density, indicating that density-dependent effects were small.

Both of our hypotheses about how invasibility should vary among habitats and with level of disturbance were refuted: riparian zones were not generally more invisable than the other wetland types, and we found no general positive correlation between level of disturbance and invasibility. The fact that we got twice as high germination when we doubled the number of sowed seeds indicates that availability of microsites for germination and seedling competition were not limiting factors at these densities, but that propagule pressure is important. Our results suggest that new plant species with sufficiently high dispersal capacity and propagule pressure will be able to invade all of the tested wetland types. As expected when using native species, we found a tendency that species had higher survival in habitats where they occur naturally and we expect plant performance to become even more habitat specific with time.

The fact that all species in our study could germinate and survive for 2 to 3 years in all three wetland habitats, indicates that temperate wetland species would be able to germinate and establish here in their respective wetland type. Many wetland plant species in northern regions may thus adjust their ranges polewards in response to a warmer climate, but for a more complete understanding of range adjustments in response to climate change, studies involving the entire life cycle of plants are needed. In reality, many species are limited by factors such as dispersal and biotic interactions, making them unable to fill their potential present or future climatic niche space (Svenning & Skov 2004). The ability of a species to adjust its range by dispersal depends not only on the dispersal capacity of the species but also on the spatial configuration of habitats being invaded. Among the wetland types tested, riparian zones should allow faster invasion across landscapes owing to their linear shape (Andersson & Nilsson 2002) and network-like properties (Grant *et al.* 2007) and riparian zones are generally more invaded than other wetland types (Crawley 1987). However, if range expansions are primarily attained by long-distance events, as suggested by the rapid spread of temperate plant species in response to warming in the early Holocene (Clark 1998; Cain *et al.* 2000), habitat configuration may be less important. Many plants, including species with poor dispersal ability have however been translocated across biogeographic barriers with the help of humans, to be used for gardening and horticulture. Many of those species may benefit from warmer climate, especially if they originate from warmer areas.

## Concluding remarks

A large part of the results in this thesis are predictions of future changes. Our calculations are based on models of runoff that takes a range of factors into account, making it likely that some aspects will be different than predicted. We do not imply that any of the specific scenarios will necessarily come true, but our results show that changes in may be large despite moderate changes in flow. The general trend is also very similar between of scenarios: it is mostly a matter of magnitude, but even with the best case scenario mainly negative changes are expected. Our projected results should not be interpreted using decimals, but with a changing climate it is highly important to estimate the direction of and general magnitude of responses. I hope that the results from this thesis will contribute to the understanding of riparian and wetland ecology and that the results will be considered for management plans and come to practical use.

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## Sammanfattning

Klimatförändringar väntas leda till en ökande global medeltemperatur under detta århundrade. Den största ökningen kommer att ske på nordliga breddgrader och för Sverige förväntas en höjning med 2,6–4,6 grader. Utöver stigande temperaturer beräknas också den årliga nederbörden öka i norra Europa och en större andel av den kommer att falla som regn istället för snö under vintern. Det kommer i sin tur att förändra vattenföringen i många vattendrag och därigenom även förutsättningarna för ekosystemen. För den boreala delen av Sverige kommer vårfloden att minska i omfattning. Medelvattenföringen däremot kan öka med upp till 24% och flödestoppar under sensommar och höst förväntas bli mer frekventa. Sannolikt kommer också de stora 100-årstopparna att komma oftare.

Strandzoner och våtmarker är områden där mängden vatten kontrollerar växtsamhällets artsammansättning. Det är därför sannolikt att dessa ekosystem är särskilt känsliga för förändrad temperatur och nederbörd. Klimatförändringarna riskerar att förändra diversiteten i de strandzoner som i dag utgör några av de mest artrika miljöerna på våra breddgrader. Förändringarna kommer även att bero på i vilken mån nya arter kommer att invadera söderifrån som en följd av det mer gynnsamma klimatet. Nya arter skulle förändra förutsättningarna för det befintliga växtsamhället och speciellt kunna missgynna arter med nordlig utbredning.

I den här avhandlingen undersöker vi hur och i vilken omfattning våtmarks- och strandekosystem kommer att förändras vid olika klimatscenarion. För att testa hur strandvegetation kan komma att påverkas av förändrade flöden utförde vi ett experiment där stora torvor av strandvegetation (70 x 100 cm) transplanterades till en annan nivå på stranden. Torvorna flyttades mellan tre olika nivåer och förändringen följdes under sex år. Sedan undersökte vi hur storleken på strandzonen, artrikedom, och utbredning av enskilda arter kan komma att förändras. Det gjorde vi genom att först relatera dessa faktorer till dagens flödesregim och sedan applicera sambanden på framtida flödesscenarion. Slutligen undersökte vi om det finns någon skillnad i invaderbarhet (ekosystemets mottaglighet för etablering av nya arter) mellan de tre vanligt förekommande våtmarkstyperna strandzoner, sumpskogar och öppna myrar. Vi utförde ett experiment där sex våtmarksarter såddes i ytor som utsatts för lätt eller kraftig störning.

Våra resultat visar att strandvegetationen kommer att reagera på förändrade flöden, men att processen är ganska långsam. Om inga ovanligt höga flöden eller torra år förekommer tar det minst tio år för artrikedom och artsammansättning att anpassas. Vegetationens biomassa kan däremot förändras fortare. Vi visar att hela strandzonen sannolikt kommer att minska i bredd men att omfattningen beror på vilket klimatscenario som används. Minskningen kommer främst att ske vid den övre mest artrika delen av stranden, där vegetationen består av strandskog och videbälten. Våra beräkningar för Vindelälven visar att 1-9 % av arterna riskerar att gå förlorade på en 100 m lång sträcka och att den rumsliga nischen för de allra flesta arterna kommer att minska. Detta innebär också att många arter kommer att bli mer sällsynta och att risken för slumpmässiga lokala utdöenden kommer att öka. Förlusterna riskerar att bli mycket större i älvar längre söderut i den boreala zonen, där förändringarna i hydrologin förväntas bli större.

I försöket om invaderbarhet grodde flest frön på myrar och stränder för alla sex arterna. Vi kunde inte se några negativa täthetsberoenden utan snarare att frömängden var väldigt viktig för antalet groddplantor och

effekten av störning var generellt låg. Överlevnaden var störst i de våtmarkstyper där arterna är vanligast. Studien visar dock att alla arter kunde gro och överleva under två till tre år i alla habitat. Det tyder på att sydliga våtmarksarter med tillräckligt bra spridningsförmåga och höga frötätheter skulle kunna invadera boreala våtmarker i ett varmare klimat.

Ett förändrat klimat kommer att medföra stora förändringar för strukturen, storleken och diversiteten av boreala våtmarksekosystem. För att bevara de artrika miljöer som fortfarande är relativt oförstörda av reglering och annan mänsklig påverkan, är det nuvarande lagliga skyddet sannolikt inte tillräckligt. Ett utökat skydd av fler områden mot olika typer av exploatering och även återskapande åtgärder som ekologisk restaurering kan därför behövas.

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Guggelito och Bus-Britta, tack, ni betyder allt...

...och snart är det sommarlov!