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



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Keywords:	Biomass, Climate change, Flooding, Productivity, Reciprocal transplant experiment, River banks, Species composition, Species richness
Abstract:	Climate change is expected to alter the magnitude and variation of flow in streams and rivers, hence providing new conditions for riverine communities. We evaluated plant ecological responses to climate change by transplanting turfs of riparian vegetation to new elevations in the riparian zone, thus simulating expected changes in water-level variation, and monitored the results over 6 years. Turfs moved to higher elevations decreased in biomass and increased in species richness, whereas turfs transplanted to lower elevations gained biomass but lost species. Transplanted plant communities were inert in their response to new hydrologic conditions. After 6 years, biomass of transplanted turfs did not differ statistically from target level controls, but species richness and species composition of transplants were intermediate between original and target levels. By using projections of future stream flow according to IPCC climate change scenarios, we predict likely changes to riparian vegetation in boreal rivers. Climate-driven hydrologic changes are predicted to result in narrower riparian zones along the studied Vindel River in northern Sweden towards the end of the 21st century. Present riparian plant communities are projected to be replaced by terrestrial communities at high elevations as a result of lower-magnitude spring floods, and by amphibious or aquatic

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	<p>communities at low elevations as a result of higher autumn and winter flows. Less area available to riparian plants is expected to result in fewer species, even if no species lose their hydrologic niches. Changes to riparian vegetation may be larger in other boreal climate regions: snow-melt fed spring floods are predicted to disappear in southern parts of the boreal zone, which would result in considerable loss of riparian habitat. Our study emphasizes the importance of long-term ecological field experiments given that plant communities often respond slowly and in a non-linear fashion to external pressures.</p>



For Review Only

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

Running title: Climate-change effects on riparian vegetation

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Keywords: biomass, climate change, flooding, productivity, reciprocal transplant experiment, river banks, species composition, species richness, water table, wetlands

Abstract

Climate change is expected to alter the magnitude and variation of flow in streams and rivers, hence providing new conditions for riverine communities. We evaluated plant ecological responses to climate change by transplanting turfs of riparian vegetation to new elevations in the riparian zone, thus simulating expected changes in water-level variation, and monitored the results over 6 years. Turfs moved to higher elevations decreased in biomass and increased in species richness, whereas turfs transplanted to lower elevations gained biomass but lost species. Transplanted plant communities were inert in their response to new hydrologic conditions. After 6 years, biomass of transplanted turfs did not differ statistically from target level controls, but species richness and species composition of transplants were intermediate between original and target levels. By using projections of future stream flow according to IPCC climate change scenarios, we predict likely changes to riparian vegetation in boreal rivers. Climate-driven hydrologic changes are predicted to result in narrower riparian zones along the studied Vindel River in northern Sweden towards the end of the 21st century. Present riparian plant communities are projected to be replaced by terrestrial communities at high elevations as a result of lower-magnitude spring floods, and by amphibious or aquatic communities at low elevations as a result of higher autumn and winter flows. Less area available to riparian plants is expected to result in fewer species, even if no species lose their hydrologic niches. Changes to riparian vegetation may be larger in other boreal climate regions: snow-melt fed spring floods are predicted to disappear in southern parts of the boreal zone, which would result in considerable loss of riparian habitat. Our study emphasizes the importance of long-term ecological field experiments given that plant communities often respond slowly and in a non-linear fashion to external pressures.

Introduction

Global mean annual temperature has increased by 0.7°C during the 20th century (IPCC 2007). Models of climate change predict that temperature will continue to increase during the 21st century. The highest warming will take place at high northern latitudes (IPCC 2007), calling for studies of how northern ecosystems will respond. At the regional scale, species range shifts are predicted (Saetersdal *et al.* 1998; Thuiller *et al.* 2005; Post *et al.* 2009), but to understand ecosystem-level responses, changes in local environmental conditions need also to be considered.

Warmer climates will likely result in more precipitation in general and less precipitation falling as snow in high northern latitudes, altering the hydrology of streams and rivers (Andréasson *et al.* 2004; IPCC 2007; Woo *et al.* 2007). Stream-flow regimes in the boreal zone are strongly seasonally variable. In natural conditions they are characterized by a spring flood peak with the highest levels of the year driven by snowmelt, followed by lower summer discharge (Woo *et al.* 2007). Regionally, summer and autumn rains might create flood peaks but during winter the flow is low, primarily fed by groundwater discharge. A warmer climate will generally increase winter discharge in all types of boreal rivers since more precipitation will fall as rain (Andréasson *et al.* 2004; Woo *et al.* 2007). Earlier snowmelt will also result in earlier spring floods of lower amplitude. In accordance with these expectations, annual stream flow in high northern rivers has increased in recent decades (Peterson *et al.* 2002).

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.* 2007). In Sweden the temperature is expected to increase by an average of 2.5 to 4.6 °C by the year 2100

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3 (Andréasson *et al.* 2004). Hydrologic models predict mean annual runoff to increase by up to
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5 24 % in the boreal part of Sweden with decreased spring flood peaks, increased frequency of
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7 high flow events during autumn, and higher winter flows (Andréasson *et al.* 2004). In Arctic
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9 river systems, where prolonged periods with below-zero temperatures will still occur, the
10
11 increased precipitation might even lead to deeper snow, creating higher but earlier spring
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13 flood peaks (Dankers & Middelkoop 2008). In areas with continental climate, summer flows
14
15 are predicted to decrease as a result of increased evapotranspiration, but in other regions
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17 summer flows will increase due to higher precipitation (Woo *et al.* 2007). Rivers draining
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19 glaciers are also likely to experience increasing discharge of summer melt water.
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27 Climate-driven hydrologic changes are expected to change riverine communities since they
28
29 are controlled by the magnitude and variation in flow (Décamps 1993; Naiman & Décamps
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31 1997; Poff *et al.* 1997). We focused on riparian ecosystems, which are unusually complex,
32
33 dynamic, and diverse, and possess numerous economic, societal, and biological values
34
35 (Sharitz *et al.* 1992; Naiman *et al.* 2002). These qualities are all maintained by regular floods,
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37 and might thus change as a result of climate alterations. Riparian plant communities are
38
39 structured by differences in the hydrologic niches of species (Silvertown *et al.* 1999).
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44 Substantial changes in riparian vegetation may take place without altering the mean annual
45
46 flow, as riparian vegetation is especially sensitive to changes in minimum and maximum
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48 flows (Auble *et al.* 1994). In boreal rivers, riparian vegetation is vertically zoned according to
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50 the flooding tolerance and moisture requirements of species (Auble *et al.* 1994; Johansson &
51
52 Nilsson 2002). Floods pose stresses and disturbances to riparian plants by affecting
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54 physiological processes such as photosynthesis and respiration (Kozlowski 1984; Vervuren *et al.*
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56 2003; van Eck *et al.* 2004; Mommer & Visser 2005; Renöfält *et al.* 2007), by removing
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58 plant biomass (Bendix 1999) or burying plants under deposits of sediment or organic matter
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3 (Xiong & Nilsson 1997). These processes may enhance species richness by suppressing
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6 dominants and enhancing the colonization and survival of competitively subordinate species
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8 (Day *et al.* 1989, Pollock *et al.* 1998). However, along gradients of increasing stress and
9
10 disturbance, species richness may decline as the challenges of flooding exceed the capacity of
11
12 species. Local species richness peaks in the mid-elevation riparian shrub zone (Pollock *et al.*
13
14 1998), but the pool of riparian species is largest close to the annual high-water level (Nilsson
15
16 1983), where flood duration is short and species lacking physiological adaptations to flooding
17
18 may grow. Plant productivity also varies predictably with flood frequency and duration, with
19
20 biomass production generally increasing from spring-flood maintained communities to sedge-
21
22 dominated communities experiencing prolonged periods of inundation (Dwire *et al.* 2004). To
23
24 be able to predict how riparian vegetation will respond to climate change we addressed the
25
26 following questions:
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31 (1) How will changes in flood duration and frequency affect riparian species richness?

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33 According to hydrological models the upper part of the riparian zone will be flooded less
34
35 frequently while the lower part will experience longer periods of inundation. Changes in flood
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37 disturbance can both increase and decrease species richness depending on where the
38
39 community is situated along the disturbance continuum (e.g. Pollock *et al.* 1998). To be able
40
41 to predict changes in species richness experiments are necessary.
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45 (2) Similarly, how will the hydrologic changes alter biomass production? Biomass is
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47 expected to decrease in high to mid elevation riparian forest and shrub communities as a
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49 result of lower duration of flooding, but increase at lower elevations dominated by
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51 graminoids, where flood duration is expected to increase. This does not take into account that
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53 a warmer climate may increase plant biomass production as a result of warmer and longer
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55 growing seasons, potentially resulting in more plant litter accumulation, if not limited by
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57 water availability or flooding.
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6 Addressing these questions requires manipulating the frequency and duration of floods.
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8 However, experimental manipulation flow in streams and rivers to test scientific hypotheses
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10 are usually not an option. As an alternative, we assessed the effects of climate change on
11
12 productivity and species richness of riparian plant communities by performing a reciprocal
13
14 transplant experiment, moving vegetation turfs between different elevations in the riparian
15
16 zone. This simulated changes in the frequency and duration of floods, and we monitored the
17
18 responses over 6 years. Reciprocal transplantation is a powerful method to assess the effects
19
20 of contrasting environments on species, but it has only recently been used to assess responses
21
22 of plant communities in wetland ecosystems (Toogood *et al.* 2008). The flow of most rivers is
23
24 affected by dams and diversions (Nilsson *et al.* 2005), making it difficult to isolate the effects
25
26 of climate change on hydrology and ecosystems from effects of land-use. Therefore, we chose
27
28 to work along the seventh-order Vindel River in northern Sweden, a free-flowing tributary in
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30 the Ume River catchment. Our objective was to investigate how floodplain meadow plant
31
32 communities respond to manipulations in hydrology and litter inputs simulating those
33
34 expected as a result of future climate change. The experimental design allowed asking how
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36 long it will take for plant communities to adjust to new hydrologic conditions. The results will
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38 improve our ability to predict how and at what rate vegetation succession will occur on
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40 floodplains subject to changes in hydrology and litter inputs as a consequence of climate
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42 change.
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Methods

Study area

The experiment was conducted on a floodplain meadow along the lower reaches of the free-flowing Vindel River in northern Sweden (N 64°22', E 19°22'). The Vindel River originates in the Scandes mountain range and joins the Ume River about 30 km from the coast of the Gulf of Bothnia. The catchment area is 12 654 km² of which 5 % are lakes. The river is 455 km long and the mean annual discharge is 200 m³s⁻¹ at the confluence with the Ume River. The discharge is unaffected by dams and diversions and varies between 16 and 1787 m³s⁻¹ [mean annual minimum and maximum flows 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 river-margin vegetation is distinctly vertically zoned along the entire river. The width and plant zonation and width 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). 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 herbs. Following abandonment, riparian tree and shrub species have colonized higher elevations of these meadows. 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).

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6 The experimental site was located about 70 km upstream of the confluence between the
7
8 Vindel and Ume Rivers at 220–230 m a.s.l., and was formerly used for haymaking. The site
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10 was selected since it was a fairly large, homogenous riparian meadow with uniform soil grain
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12 size consisting of silt, located 2.5 km upstream of a stream flow gauge. The vegetation at the
13
14 site was zoned, going from communities dominated by graminoids and herbs with some older
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16 birches (*Betula pubescens*) at the top, to mid elevations dominated by *Salix* shrubs and
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18 graminoids such as *Calamagrostis canescens*, followed by herbaceous communities
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20 dominated by *Carex acuta*, *Calamagrostis canescens* and various amphibious species such as
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22 *Ranunculus reptans* at the bottom. The annual growing season (days where the average
23
24 temperature exceeds +5°C) is about 150 days (period 1961–1990, SMHI).
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31 *Layout of plots and treatments*

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33 A total of 96 plots were distributed at three elevations (Fig. 1), corresponding to the riparian
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35 belts of forest, shrub and graminoids (Nilsson 1983). The vertical difference in elevation was
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37 0.55 m between high and middle plots, and 0.90 m between middle and low plots. To simulate
38
39 changes in the flood regime, we transplanted vegetation between elevations in June 2000.
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41 Each plot was 70x100 cm in size and was excavated to a depth greater than the rooted zone.
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43 Excavated turfs were either carefully put on metal cradles with handles to allow transport to
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45 one of the other two elevations with minimal disturbance to the soil, or rotated 180° and put
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47 back into their original positions to evaluate the effect of excavation. The remaining plots
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49 were left intact serving as controls. The meadow was divided into four blocks, with two
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51 replicates of each treatment per block. Thus, eight replicates that each consisted of 12 plots,
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53 i.e. three elevations with the four treatments each (Fig. 1). To simulate increased litter
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55 production as a consequence of potential increase in plant productivity due to longer and
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3 warmer growing seasons, we applied 2000 g m⁻² of riverborne litter in 2001 and 2002 to half
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5 of the plots, one of the replicates in each block. The litter consisted of graminoids and forbs
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7 and tree leaves, collected from the riparian zone in nearby reaches of the Vindel River during
8
9 spring flooding, and dried at room temperature. To keep the applied litter in place a 5 cm high
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11 boundary marker of chicken net was placed around each transplanted plot. To control for an
12
13 eventual effect on vegetation of this net, it was applied also to plots without added litter. At
14
15 each level a pressure transducer data logger (Divers, van Essen Instruments Limited) was
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17 placed in a well of polystyrene plastic inserted into the ground to measure water level. The
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19 difference in ground surface elevation between the loggers was measured using a total station
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21 [Geodolite[®] 506, Geotronics (Trimble), Sweden].
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29 *Sampling*

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31 We recorded the frequency of all vascular plant species in each plot using the point touch
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33 method (16 points in a 50x50cm area, 10 cm from the edge of the plots, to minimize edge
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35 effects; Fig. 1) in August each of the years 2000–2003, 2005 and 2006. Every species
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37 touching the stick was recorded once at each point, i.e. the maximum score was 16 per plot. In
38
39 addition, the presence of any additional species in the plot was recorded. Plant biomass was
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41 harvested from subplots (15x20 cm) nested within each plot (Fig. 1) every year species
42
43 richness was recorded. After harvest, biomass was dried at 60°C for 72 h and weighed. A
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45 subset of 24 plots, representing all treatments, was used for soil sampling for chemical
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47 analysis and for measuring soil moisture in 2000–2002. Soil moisture was measured twice
48
49 each season with plaster cubes in the ground and a soil moisture meter (Model 14.22,
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51 Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands). Water levels were measured
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53 continuously with the data loggers from 2000 to 2003.
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3 The definition of species follows the taxonomy in Krok and Almquist (1994). In the following
4 cases two or more species were treated as one taxon: *Carex juncella* + *C. nigra*, *Hieracium*
5 spp., *Hierochloë hirta* + *H. odorata*, *Luzula multiflora* + *L. sudetica*, *Poa* spp., *Salix borealis*
6 + *S. myrsinifolia* + *S. phylicifolia*, and *Taraxacum* spp.
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15 *Data analysis*

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17 Flood duration and frequency for the entire sampling period were quantified by correlating
18 the logger data for the first 4 years with water level measurements made by the SMHI at the
19 gauge in Granåker 2.5 km downstream in the same tranquil reach; there were no intervening
20 steps or rapids. By comparing instrumental water level records from the Granåker gauge and
21 the experimental site date by date, we constructed a calibration curve by which the gauge data
22 could be used to generate water-level data for each elevation at the experimental site in
23 Strycksele. By interpolating gauge data, we estimated the flooding regime for 2004–2006 for
24 all plots, to supplement the 2000–2003 water-level data.
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39 Simulations of future streamflow for the period 2071–2100 at the nearby gauge were obtained
40 from SMHI (Andréasson *et al.* 2004). They were calculated using the Rossby Centre Regional
41 Atmosphere-Ocean Model (RCAO) and the runoff model HBV developed by SMHI, using
42 data from two general circulation models: HadAM3H from the Hadley Centre of the UK
43 Meteorological Office and ECHAM4/OPYC3 from the Max-Planck Institute for Meteorology
44 in Hamburg. The general circulation models were run with data according to the A2 and B2
45 IPCC emission scenarios (Nakicenovic & Swart 2000), where the A2 scenario results in larger
46 increases in greenhouse gas emissions than the B2 scenario (for detailed description of the
47 simulation models, see Andréasson *et al.* 2004). We used the same method as above to
48 interpolate projected future water-level records at the gauge to water levels at the study site.
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6 To evaluate the effects of plot trenching, such as root damage and soil disturbance, we
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8 compared plots that were excavated, removed and put back into their original position after
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10 rotating 180°, with control plots at the same elevation. We used mixed-effects ANOVAs to
11
12 analyze variation in biomass and species richness depending on trenching (excavated or not)
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14 and elevation (treated as fixed factors), with experimental block as a random factor. The
15
16 effects of litter addition were evaluated with factorial ANOVA with original and target
17
18 elevations and litter addition as fixed factors. The tests were performed separately for each
19
20 year of vegetation sampling. The effect of blocking the experiment was found to be weak (i.e.
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22 variation within blocks was similar to between-block variation), and hence we did not include
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24 block as a factor in these and subsequent ANOVAs.
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32 To test the effect of changed frequency and duration of flooding on species richness and
33
34 biomass, we compared turfs that were transplanted to a new elevation with trenched turfs
35
36 remaining in their original position at both the original and target levels of the transplanted
37
38 turfs. To evaluate the effect of transplantation, we compared the relative changes in biomass
39
40 and species richness between 2000 and 2006, as well as differences between treatments the
41
42 final study year (2006), using one-way ANOVA (with treatment as a factor) and evaluated
43
44 significant differences among treatments using Tukey's post-hoc tests of honest significant
45
46 difference ($\alpha = 0.05$). The treatment groups were transplanted turfs and excavated control
47
48 plots at the origin and target levels of transplants. We made separate tests for each exchange
49
50 of transplants between levels (i.e. between high and low levels, high and mid levels, and mid
51
52 and low levels; Fig. 1). When litter addition was included as a factor in these ANOVAs, it did
53
54 not significantly ($P > 0.05$) affect biomass and species richness, and was dropped during model
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56 simplification.
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6 To evaluate changes in community composition as a result of transplantation, we used
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8 Detrended Correspondence Analysis (DCA; ter Braak & Šmilauer 1998). To analyze whether
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10 transplanted turfs resembled the species composition of turfs at the original elevation, or had
11
12 attained a species composition similar to the target levels, we tested for differences among
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14 treatments in the first axis site scores of the DCAs, using one-way ANOVAs with treatment
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16 (transplantation vs. excavated controls at the original and target levels) as a factor. We used
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18 untransformed species frequency data from the first and final years of the experiment in the
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20 analyses, detrended by segments and downweighting rare species. Significant differences
21
22 among treatments were evaluated using Tukey's post-hoc tests. We made separate tests for
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24 each exchange of transplants between levels as above. We also tested for differences in soil
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26 moisture between elevations (high, mid and low) in the riparian zone with a one-way
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28 ANOVA and Tukey's post-hoc test. All statistical analyses were performed in the statistical
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30 package R (R Development Core Team 2006), except for the ordination which was done in
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32 Canoco version 4 (ter Braak & Šmilauer 1998).
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Results

Present and projected future hydrologic regimes

During the experiment, the low elevation was flooded every year, the mid elevation was flooded in 5 of the 7 years, and the high elevation was only flooded in 2004 and 2005 (Table 1). Flood duration also varied among years (Fig. 2). In 2001, flood duration was twice as long at the low elevation well compared to the other years, or 81 days compared to 16–40 days the other years. Both duration and frequency during the experimental period (2000–2006) were lower compared to the reference period 1961–1990 (Table 1), which is the period used by SMHI as a baseline to calculate future scenarios. The largest difference was at the low elevation well, with 20 days shorter mean flood duration per year during the experiment (Table 1). The projections of future hydrologic conditions predicted shorter flood duration and longer flood return times at the high riparian elevation in 2071–2100 compared to the normal period 1961–1990 (from 2.1 to up to 7.5; Table 1). The mid elevation will also be flooded less often and with less duration, but the changes are smaller. The low elevation is projected to still be flooded every year with similar or longer durations compared to 1961–1990 (Table 1). Soil moisture increased towards lower elevation in the riparian zone (mean \pm 1SE, high 54.9 ± 2.2 , mid 61.8 ± 1.0 , low 67.9 ± 1.8 ; $F = 8.5$, $P = 0.002$, one-way ANOVA with elevation as a factor).

Responses of riparian vegetation to changes in hydrology

The only significant effect of trenching was found on biomass in 2001. This year, biomass in the trenched plots at low elevations was significantly lower than in the controls (178 ± 35 g compared to 554 ± 84 g, $P < 0.0001$, mixed-effects ANOVA), and the trenched plots at high elevation had significantly more biomass compared to the controls (388 ± 66 g compared to 219 ± 42 g, $P = 0.024$). We found no significant differences between trenched and control plots

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3 in species richness for any year or elevation ($P > 0.05$). Thus, after an initial biomass
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5 response, trenching *per se* did not significantly affect the vegetation features. In the remaining
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7 analyses, we used the trenched plots as controls for the transplantation treatments. Litter
8
9 addition significantly reduced biomass in 2002, which was the second and last year litter was
10
11 applied (Table 2), and significantly reduced species richness in 2003. Litter addition reduced
12
13 biomass and species richness at all elevations in the riparian zone. No statistically significant
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15 effects of litter addition were detected in any of the following years.
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22 The overall effect of the transplantation experiment was that turfs transplanted to higher
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24 elevations decreased in biomass and increased in species richness, whereas turfs transplanted
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26 to lower elevations gained in biomass but lost in species richness (Figs 3–5), although not all
27
28 changes following transplantation were significant. Turfs transplanted from high to low
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30 elevations increased in biomass compared to the high elevation controls and turfs transplanted
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32 to mid elevations ($P < 0.05$, one-way ANOVA; Fig. 3a). Comparing biomass between years
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34 shows that both transplanted turfs and the low-elevation controls decreased substantially in
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36 biomass from 2000 to 2001 (Fig. 4a). The low-elevation controls and the turfs transplanted to
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38 low elevations successively increased in biomass thereafter, while the turfs transplanted from
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40 low to high elevations remained low during the remainder of the experiment. The final year of
41
42 the experiment, the plots transplanted between high and low elevations did not differ in
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44 biomass compared to the target elevation controls, but differed significantly from their
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46 original values (Fig. 4a). The relative change in biomass did not differ among plots
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48 transplanted between mid and low elevations (Fig. 3c and e; $P > 0.05$), and there were no
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50 significant differences in biomass between them the last year (Fig. 4b and c).
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3 We found between four and five times as many species on high and mid elevation controls
4 compared to low elevation controls ($P < 0.05$, one-way ANOVAs and Tukey's tests; Fig. 5a
5 and c). In contrast, we found no difference in species richness between high and mid
6 elevations, and turfs transplanted between mid and high elevations did not change in species
7 richness ($P > 0.05$; Figs 3b and d and 5b). Turfs from high elevations lost species when
8 transplanted to low elevations ($P = 0.002$, one-way ANOVA and Tukey's tests), but did not
9 differ from high elevation controls if transplanted to mid elevations ($P > 0.05$; Fig. 3b).
10 Transplants originating from the mid elevation did not differ in species from mid-elevation
11 controls, but there was a difference in species-richness change between the ones moved to
12 high vs. low elevations ($P = 0.014$), since turfs moved up gained and turfs moved down lost
13 species (Fig. 3d). Turfs transplanted from low to mid and high elevations gained significantly
14 more species compared to low elevation controls ($P < 0.01$; Fig 3f).

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34 The composition of the transplanted plant communities adjusted slowly to the hydrologic
35 conditions at the target elevations: Only the turfs transplanted from high to low elevations
36 were statistically indistinguishable in species richness and composition from low elevation
37 controls 6 years after transplantation (Figs 5a and 6a). In all other cases, species richness or
38 composition still differed significantly. Changes in species richness occurred gradually during
39 the experiment (Fig. 5): Turfs transplanted from high to low elevation lost species
40 successively and did not differ in species richness from the low elevation controls at the end
41 of the experiment ($P = 0.282$; Fig. 5a). Although turfs transplanted from low to high gained
42 species over time, they still had fewer species compared to high elevation controls at the end
43 of the experiment ($P = 0.031$; Fig. 5a). Turfs transplanted from mid to low elevations were
44 intermediate in species richness between the low and mid elevation controls ($P = 0.040$, Fig.
45 5c). Turfs transplanted from low to mid elevation gained species over time and had more
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3 species than the low elevation controls ($P = 0.015$), and did not differ significantly in richness
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5 from the controls of their new elevation ($P = 0.099$, Fig. 3c).
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10 No species other than those already growing in the meadow at the start of the experiment
11
12 invaded the turfs during the 6 years; exotic species were absent. In all ordinations of the site
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14 scores based on species data, the first axis was strong with eigenvalues ranging between 0.50
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16 and 0.87 (Fig. 6), mainly representing the riparian elevation gradient. The control plots of the
17
18 three different elevations were all significantly different in community composition from each
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20 other, both the first and last year of the experiment ($P < 0.05$, one-way ANOVA; Fig. 6).
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24 Although the site scores of the transplants had become more similar to the target elevation
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26 during the course of the experiment, only the transplantation from high to low was
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28 statistically indistinguishable from the community composition of control plots at the new
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30 elevation ($P > 0.05$, one-way ANOVA; Fig. 6a). In the remaining cases, species composition
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32 of the transplants was intermediate between original and target levels (Fig. 6b, d and e), or
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34 was statistically similar to the original levels (Fig. 6c and f).
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Discussion

Our experiment demonstrates that riparian-plant communities will change in response to the hydrologic alterations expected as a result of climate change. This study also shows the importance of conducting long-term field experiments (Milchunas & Lauenroth 1995). Plant communities 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. However, rare events such as unusually large floods or droughts may result in non-linear vegetation responses (Jentsch *et al.* 2007).

Hydrology

Flood duration during the experiment for the mid and high elevation plots was in many respects intermediate between the normal period 1961–1990 and the projections for 2071–2100, implying that the observed warming during the last decades has led to hydrological trends going in the direction of the changes expected at the end of the century as a result of warming (Peterson *et al.* 2002). We conducted the experiment during a period which was drier and with shorter floods at all elevations compared to 1961–1990 (Table 1). Although inundation duration at the low elevation in 2001 was long in comparison with other years during the experiment, lasting from May to July, it was close to the average for 1961–1990.

Effects of trenching

The fact that the only significant effect of trenching was on biomass the second year suggests that excavation had limited effects and that excavated plots could be used as realistic controls for transplantation effects. The effect of trenching on biomass was probably caused by damage to below-ground plant parts. The fact that high-elevation trenched turfs had

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3 significantly more biomass than the controls in 2001, may be due to reduced soil competition
4 from neighbouring plants outside the plots. Coomes & Grubb (2000) suggested that root
5 trenching would enhance growth when nutrients and/or water are limiting, and found support
6 for this hypothesis in a review of experiments. In contrast, where soils are relatively rich and
7 droughts are uncommon, trenching effects were weak or absent (Coomes & Grubb 2000). The
8 reduced biomass on the low-elevation transplants was likely a response to the combined effect
9 of long duration of inundation in 2001 and lower tolerance to flooding after root damage.
10 Complete submergence slows down growth even in inundation-tolerant species (Johansson &
11 Nilsson 2002; Voesenek *et al.* 2006) and water entrance into root aerenchyma following
12 trenching might have further reduced growth. Also the turfs transplanted down from the high
13 and mid elevations decreased substantially in biomass the same year (Fig. 5).
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32 *Effects of hydrologic changes*

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34 Why did biomass generally increase when turfs were transplanted to lower elevations?
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36 Growth at low elevations might have been enhanced by environmental conditions, such as
37 higher soil moisture, or species on transplanted turfs were replaced with species that grow
38 larger. In general, above-ground biomass of herbs and graminoids is high in low-lying
39 riparian and other wetland plant communities where light availability is high and water does
40 not limit growth (strongly nutrient limited communities excepted). The fact that biomass
41 increased successively from 2001 to 2006 in plots transplanted from high to low elevations
42 suggests that successive species replacement was the cause. In 2005 these plots were
43 dominated by *Calamagrostis canescens* and *Carex acuta* (on average 96% of the total
44 biomass). Both of these species were absent before transplantation. In contrast, the reason
45 why turfs transplanted from low to high elevations decreased in biomass the first year after
46 transplantation and remained low thereafter is better explained by the change in external
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3 conditions. The two species dominating turfs of low origin, *Calamagrostis canescens* and
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5 *Carex acuta*, remained high in frequency at high elevations, but decreased in biomass
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7 production, dropping from 206 g to 74 g and 260 g to 17 g, respectively, between 2002 and
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9 2005, potentially as a result of drought stress. In the long run, they are likely to be
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11 outcompeted by more drought-tolerant species, given the existence of a trade-off between
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13 flooding and drought tolerances (Luo *et al.* 2008).
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20 The slow adjustment in species composition following transplantation was probably caused
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22 by the ability of many species to tolerate hydrologic conditions distinct from those in
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24 unmanipulated systems (van Eck *et al.* 2004). The persistence of many species likely delayed
25
26 or inhibited establishment of species better adapted to the conditions at the target elevations.
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28 Even in the case of transplanting from high to low elevations, where one might expect that
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30 flood duration would exceed the tolerance of high-elevation species, species losses occurred
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32 gradually over many years (Fig. 5a). Thus, long-term experiments are needed to evaluate the
33
34 potential effects of hydrologic change on riparian ecosystems. Most ecological field
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36 experiments rarely last more than 3 years, which may be inadequate to draw conclusions
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38 about mechanisms controlling natural ecosystems, and treatment effects may change with
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40 time (Milchunas & Lauenroth 1995). Even our 6-year study was too short for plant
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42 communities to fully adjust to the new conditions imposed by the experiment.
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51 Catastrophic events, such as hurricanes or floods, can trigger permanent changes to
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53 ecosystems by causing widespread mortality, allowing new species to establish. Flooding
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55 events of exceptional duration have been shown to severely decrease species richness in
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57 riparian zones (Renöfält *et al.* 2007) and alter limits of riparian vegetation belts (Vervuren *et*
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59 *al.* 2003; van Eck *et al.* 2004). If such an event had occurred during our experiment, rapid
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3 adjustments in species composition may have resulted. The importance of events rather than
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5 gradual changes in biotic responses to climate change has recently been emphasized (Jentsch
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7 *et al.* 2007).
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10 11 12 *The future of riparian vegetation in the Vindel River*

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15 Combining the results of the transplant experiment and projections of future stream flows, we
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17 may predict likely responses of riparian vegetation to climate-driven hydrologic changes. The
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19 high riparian elevations in the experiment are projected to experience less frequent flooding
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21 (Table 1) and are expected to shift into terrestrial forest communities likely to lose most
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23 riparian species with time. Differences in species richness between riparian and terrestrial
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25 plant communities in the region are dramatic, with forest understories being dominated by a
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27 few dwarf-shrub species (Nilsson & Jansson 1995). The boundary between riparian and
28
29 terrestrial plant communities is generally sharp, occurring over a few decimetres in elevation
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31 and coinciding with the limit of floods occurring every second year (Nilsson 1983). For the
32
33 middle-elevation communities, the projected frequency of flooding resembles present ones at
34
35 the high elevation. Hence, the transplantation of turfs from middle to high elevation is
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37 relevant to predict likely effects of climate change to mid-elevation plant communities. There
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39 were no significant responses in biomass or species richness of mid-to-high transplants,
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41 implying that mid-elevations will mainly change in species composition to constitute the
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43 highest part of the regularly flooded riparian zone, representing a decline in the area of
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45 species-rich spring-flood communities.
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55 All four climate-change scenarios predict an overall increase in river runoff in the boreal part
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57 of Sweden between 1961–1990 and 2071–2100 (Andréasson *et al.* 2004). The largest flow
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59 increases will occur outside the growing season when water levels are below summer low
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3 water-levels coinciding with the lower limit of continuous *Carex* vegetation (Fig. 7), and are
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5 thus expected to primarily impact amphibious plant communities. However, low-elevation
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7 *Carex* communities may become flooded any time of the year in the future, with effects
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9 difficult to predict. For example, ice disturbance during winter floods may become common.
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11 If inundation of low-elevation, *Carex*-dominated communities would increase as suggested in
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13 the more extreme projections (Fig. 7), present communities may become replaced by
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15 amphibious plant communities. The low elevation was inundated on average 20 days shorter
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17 per year during the experiment compared to the period 1961–1990 (37.4 days compared to
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19 57.0 days; Table 1), implying that the contrast between present and projected future
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21 conditions is larger than shown in Fig. 7. To conclude, we predict that climate-driven
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23 hydrologic changes will result in narrower riparian zones along the Vindel River, with present
24
25 riparian-plant communities being replaced by terrestrial communities at the top and by
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27 amphibious or aquatic communities at the bottom. Given strong species-area relations, less
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29 area available to riparian plants is expected to reduce species richness, even if no species lose
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31 their hydrologic niches.
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41 *Predicting the effects of climate change in different boreal regions*

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43 Hydrologic changes caused by a warmer climate are expected to vary across boreal and Arctic
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45 regions (Woo *et al.* 2008) as a result of regional differences in climate change and differences
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47 in characteristics between catchments. The hydrologic response will vary depending on the
48
49 proportion of precipitation expected to fall as snow in the future, the overall trend in the
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51 amount of precipitation, and the balance between precipitation and evapotranspiration (Woo
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53 *et al.* 2008). Most northern rivers will get a significant proportion of the precipitation as snow
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55 also in the future, either because they lie in the far north or because they drain high mountain
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57 ranges. Effects of hydrologic change on such rivers are expected to be similar to the ones
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3 predicted for the Vindel River, with reductions in spring flood height and higher winter flows.
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5 The magnitude of change is expected to vary latitudinally, with the smallest changes in
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8 northernmost rivers. High Arctic rivers may even experience higher spring floods as a result
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10 of higher precipitation and more snow accumulation.
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15 Rivers in the southern parts of the boreal zone with catchments lacking large alpine areas will
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17 experience significant decreases in the proportion of precipitation falling as snow. The
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19 qualitative hydrologic changes will be similar to the Vindel River, but be more extreme:
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22 Spring floods will have lower magnitudes or disappear, resulting in losses or reductions in the
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24 area of riparian forest communities, with subsequent losses in riparian species richness. In
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26 addition, water-levels will vary less among seasons, with higher winter flows, resulting in
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28 upward displacements of low-elevation riparian zonation, amphibious and aquatic plant
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30 communities replacing herbs and graminoids. In boreal continental-climate regions, warming
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32 is expected to lead to more extreme summer humidity deficits, resulting in decreased summer
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34 flows and more drought stress, which may reduce riparian biomass production and alter
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36 competitive relations among species. This might correspond to transplanting turfs to higher
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38 elevations, and hence result in biomass losses and local species-richness increases. However,
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40 we do not know how the effect of summer droughts will combine with other climate-change
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42 effects, such as reduced spring flooding or higher frequency of autumn floods.
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51 Increases in the occurrence of major rain storms have been implicated as a result of warming
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53 (Ilg *et al.* 2008). Andréasson *et al.* (2004) predicted a general increase in the frequency of
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55 100-year floods in autumn for northern Sweden at the end of the century. Given that extreme
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57 floods of long duration have long-lasting effects on riparian plant communities, e.g. by
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59 causing extinctions of flood-sensitive species (Renöfält *et al.* 2007), increases in the
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3 frequency of such events may have profound effects. If more frequent than the recovery time,
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5 a reduction in average diversity is expected.
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10 Riparian plant communities make up a significant proportion of regional plant diversity in
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12 boreal landscapes (Nilsson & Jansson 1995; Renöfält *et al.* 2005), and the predicted losses in
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14 the area of riparian zones may thus have landscape-level consequences. A number of actions
15
16 may be taken to reduce the risk of riparian species loss. First, remaining species-rich areas
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18 may be managed to ensure long-term viability of component species. Second, streams and
19
20 rivers degraded by dams and channelization may be restored to increase the abundance of
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22 riparian species. Third, further studies are required to identify species especially at risk, for
23
24 which actions to maintain their population size may be warranted. Specifically, information
25
26 about the hydrologic requirements of individual riparian plant species is needed to predict
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28 their climate-change responses. Finally, riparian zones perform many ecosystem functions
29
30 important for other landscape elements, such as supplying wood and leaf litter to aquatic
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32 habitats and acting as a buffer against flows of matter and pollutants from terrestrial areas to
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34 streams (Naiman *et al.* 2005). Elucidating how these riparian functions are affected by
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36 climate-driven hydrologic change is a priority area for research.
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26 vegetation: a review. *Botanical Review*, **63**, 240–264.
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Table 1 Flooding regime for each elevation. Values from our study and from 1961–1990 were from data loggers or a nearby gauge, whereas the four scenarios for 2071–2100 were calculated from hydrologic data presented by the Swedish Meteorological and Hydrological Institute (Norrköping, Sweden). RT = Return time, Duration = number of flooded days per year. Model abbreviations are explained in the Methods section.

Period	Years	Riparian elevation								
		Low			Mid			High		
		RT	Duration		RT	Duration		RT	Duration	
			mean	range		mean	range		mean	range
<i>Observed data</i>										
2000 – 2006	7	1	37.4	16–81	1.4	6.9	0–14	3.5	1.7	0–7
1961–1990	30	1	57.0	28–100	1.3	9.7	0–26	2.1	2.8	0–12
<i>Models</i>										
ECHAM4-B2	30	1	67.2	30–108	1.6	6.1	0–27	6.0	1.7	0–22
HadAM3H-B2	30	1	58.0	28–99	2.3	5.0	0–26	7.5	1.3	0–21
ECHAM4-A2	30	1	75.2	29–126	2.5	4.4	0–23	7.5	1.0	0–10
HadAM3H-A2	30	1	56.0	18–95	2.7	2.9	0–24	7.5	0.9	0–10

Table 2 Effects of transplantations and the litter addition of 2001 and 2002, factorial ANOVA. Df for 2002–2006 is the same as for 2001. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

Source of variation	2000		2001		2002	2003	2005	2006
	<i>df</i>	<i>F</i>	<i>df</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>
<i>Species richness</i>								
Origin of turf	2	61.7 ***	2	17.2 ***	24.6 ***	26.5 ***	15.9 ***	16.4 ***
Target of turf	2	1.9	2	3.8 *	13.2 ***	12.1 ***	35.8 ***	39.9 ***
Litter addition			1	3.2	2.9	5.1 *	1.3	0.3
Origin x Target	4	0.9	4	0.3	0.7	0.8	1.0	1.6
Origin x Litter			2	0.7	0.2	0.3	0.5	1.4
Target x Litter			2	0.7	1.2	0.0	0.4	0.4
<i>Biomass</i>								
Origin of turf	2	3.9 *	2	0.2	1.4	4.6 *	0.6	1.1
Target of turf	2	5.0 **	2	8.9 ***	4.3 *	8.1 ***	7.9 ***	20.7 ***
Litter addition			1	1.9	4.2 *	0.1	0.9	0.3
Origin x Target	4	0.5	4	3.6 *	2.7 *	1.9	1.3	0.9
Origin x Litter			2	0.0	0.2	0.5	1.7	0.3
Target x Litter			2	1.2	0.1	0.7	0.2	0.7

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3 **Fig. 1** Schematic illustration of the experimental setup showing one of eight replicates along with
4 the spatial arrangement of vegetation data sampling within a plot. Arrows indicate how turfs were
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8 transplanted between levels. There were four blocks, giving a total of 96 plots in the experiment.

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10 Only one of the subplots for biomass sampling was harvested each year.
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3 **Fig. 2** Number of days of flooding per year at each elevation in the riparian zone during the
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5 experiment.
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3 **Fig. 3** Relative changes in biomass (a, c and e) and species richness (b, d and f) between 2000 and
4 2006 (means \pm 2SE) compared among turfs from a specific level of origin (high, mid and low)
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6 depending on their target level after transplantation (high, mid and low). Lowercase letters indicate
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8 significant differences between the responses of the turfs to the new elevation according to one-way
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10 ANOVAs and post-hoc tests (Tukey's honest significant difference; $P < 0.05$).
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3 **Fig. 4** Temporal change in biomass per plot (mean \pm SE) transplanted between (a) high and low,
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5 (b) high and mid, and (c) mid and low levels. Treatments are denoted according to their elevation in
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7 the riparian zone (low, mid and high transplantation controls), or between which levels they were
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9 transplanted (e.g. high to low). The plots were not sampled in 2004. Lowercase letters indicate
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11 significant differences among treatments the final year according to one-way ANOVAs and post-
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13 hoc tests (Tukey's honest significant difference; $P < 0.05$).
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3 **Fig. 5** Temporal change in species richness per plot (mean \pm SE) transplanted between (a) high and
4 low, (b) high and mid, and (c) mid and low levels. Treatments are denoted according to their
5 elevation in the riparian zone (low, mid and high transplantation controls), or between which levels
6 they were transplanted. The plots were not sampled in 2004. Lowercase letters indicate significant
7 differences among treatments the final year according to one-way ANOVAs and post-hoc tests
8 (Tukey's honest significant difference; $P < 0.05$).
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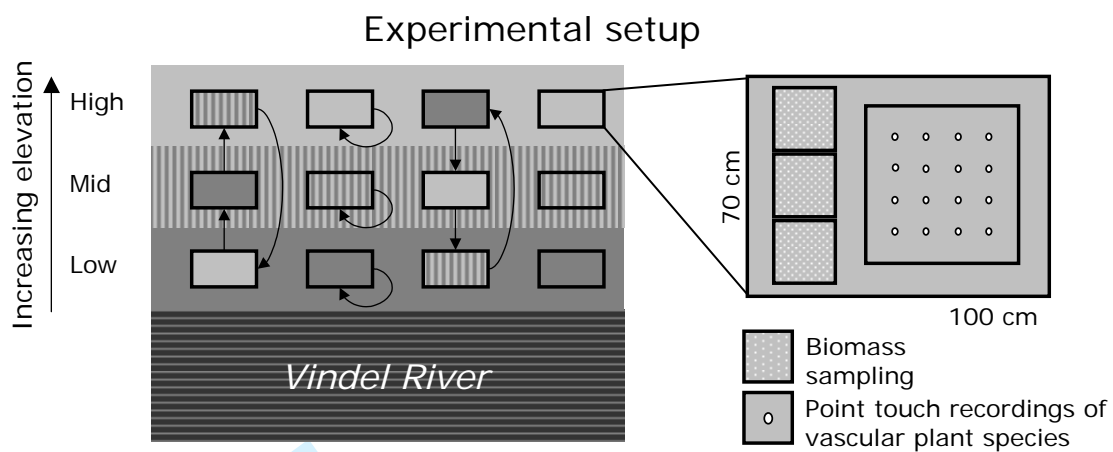
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3 **Fig. 6** Plots of site scores from the first two axes of detrended correspondence analyses showing
4 the community composition of transplanted turfs in 2000 (open symbols) and in 2006 (filled
5 symbols). Turfs from 2006 with the same treatment are enclosed, with solid lines indicating
6 controls and dashed lines turfs transplanted between two levels. Lowercase letters indicate
7 significant differences between groups along axis 1 according to one-way ANOVAs and post-hoc
8 tests (Tukey's honest significant difference; $P < 0.05$). Eigenvalues for axis 1 were: (a) 0.87, (b)
9 0.87, (c) 0.50, (d) 0.55, (e) 0.61 and (f) 0.70.
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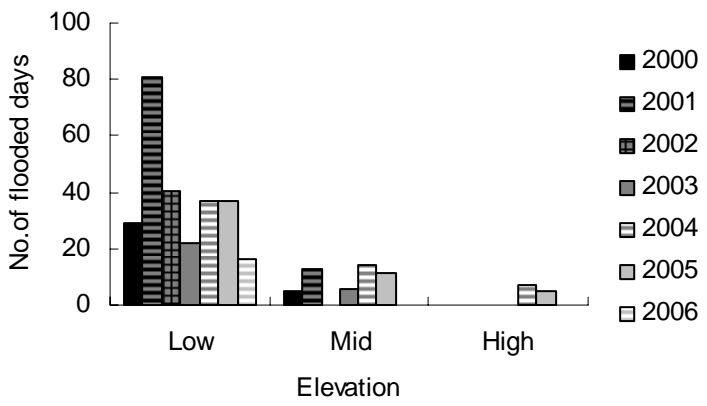
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3 **Fig. 7** Average number of flooded days per month calculated from 30 year periods, based either on
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5 measured values for the period 1961–1990 (black line) or projected values for the period
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7 2071–2100 according to climate change scenarios (gray lines). Climate models and scenarios are
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9 explained in the Methods section.
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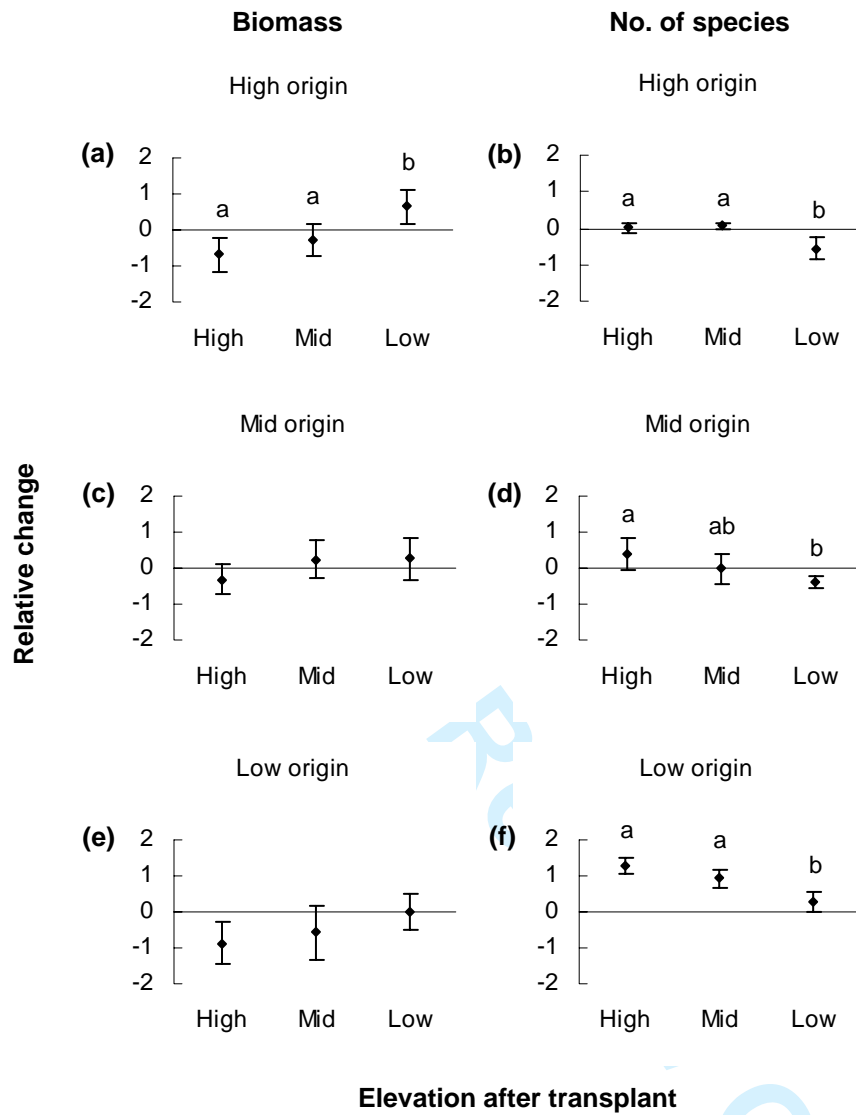


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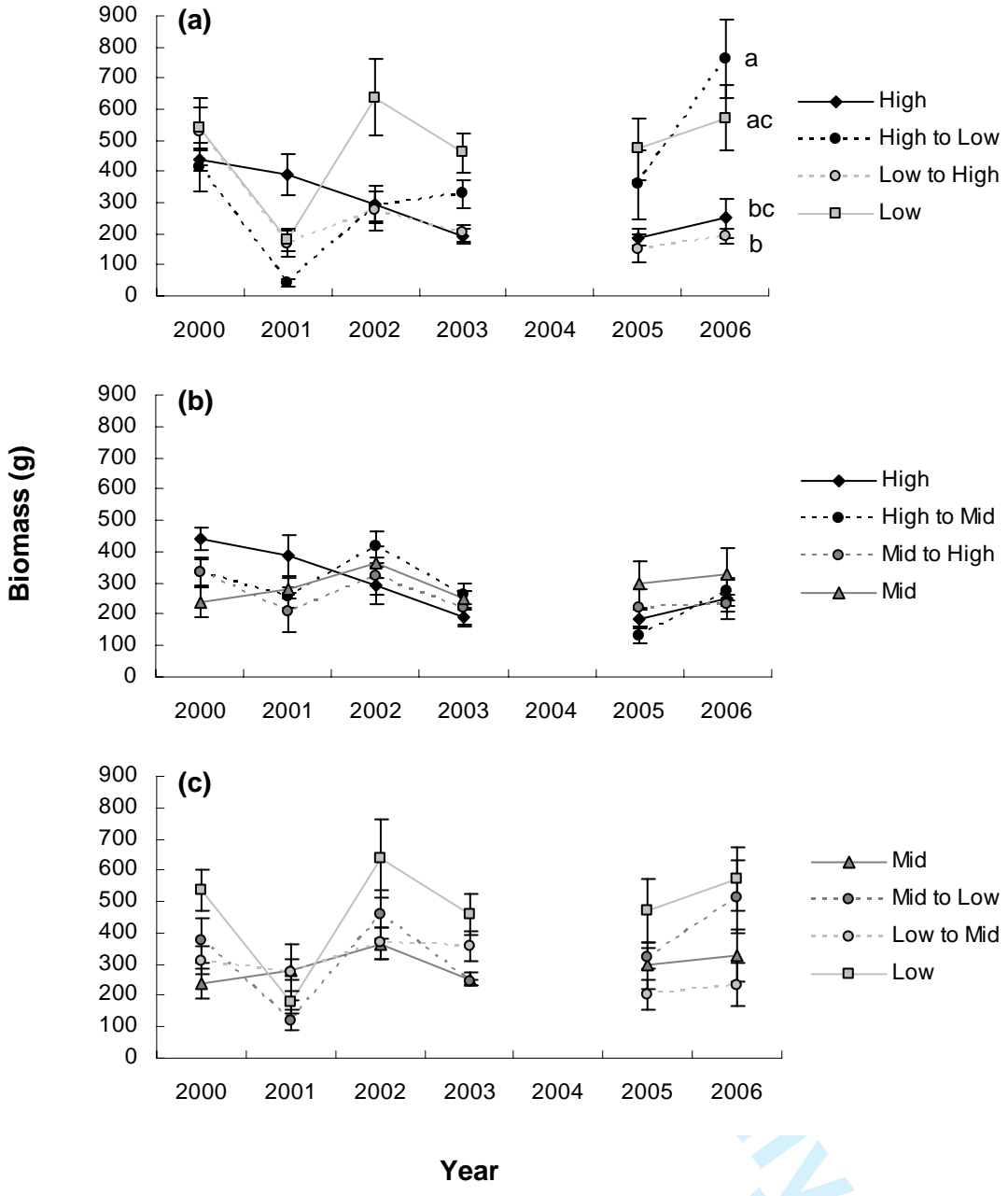
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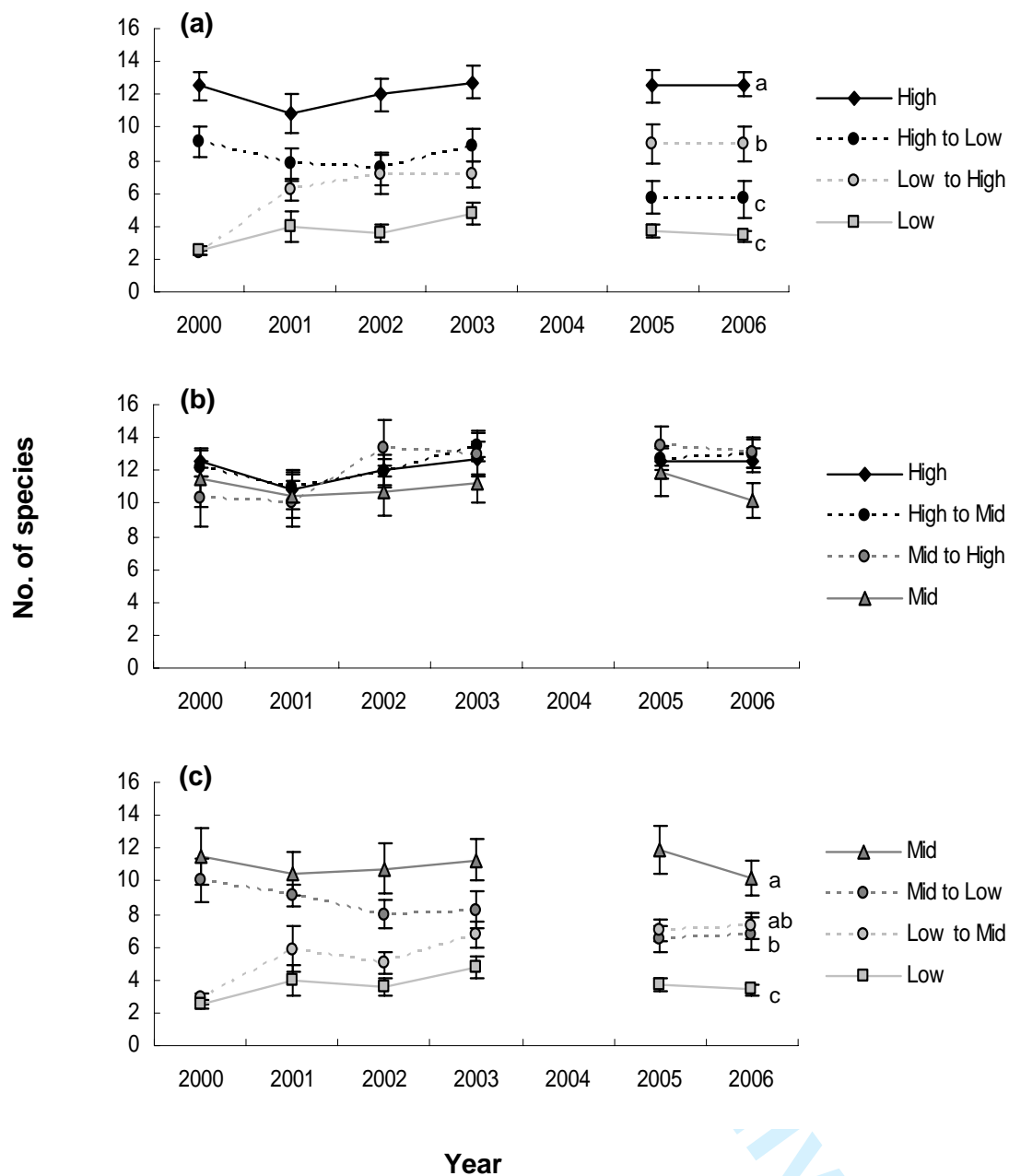


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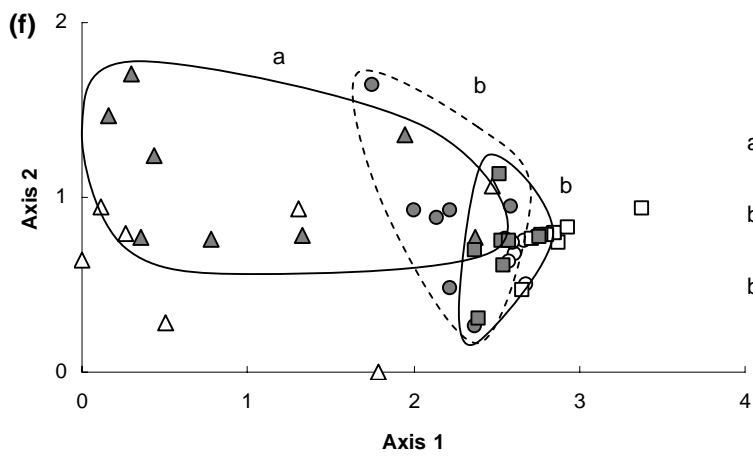
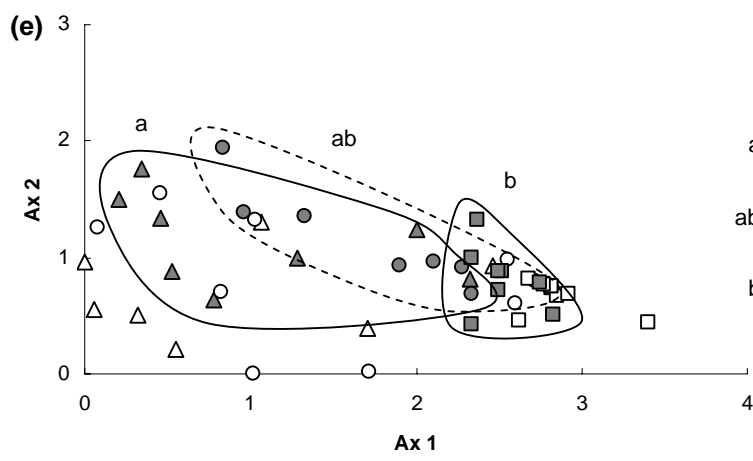
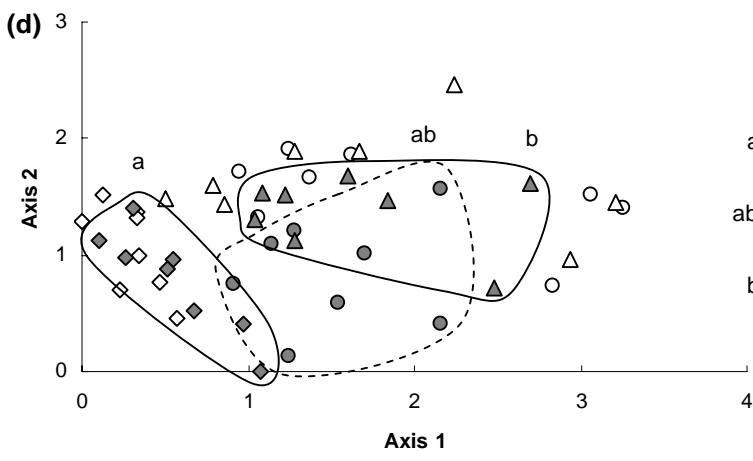
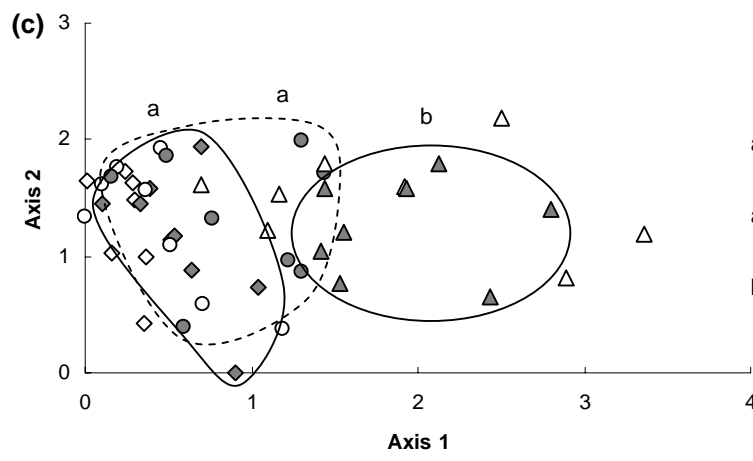
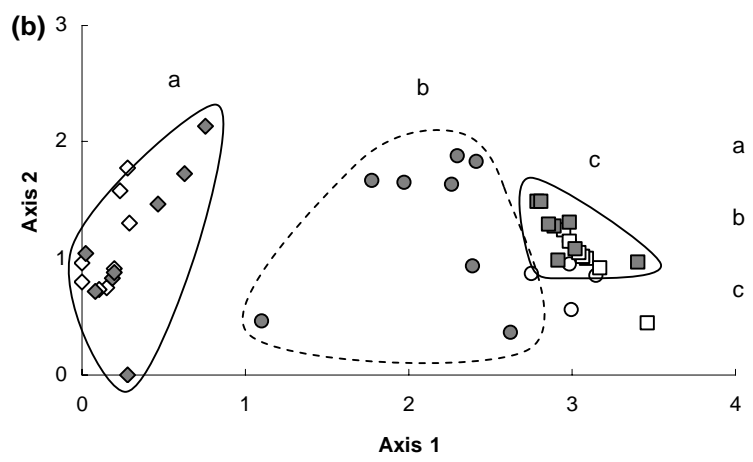
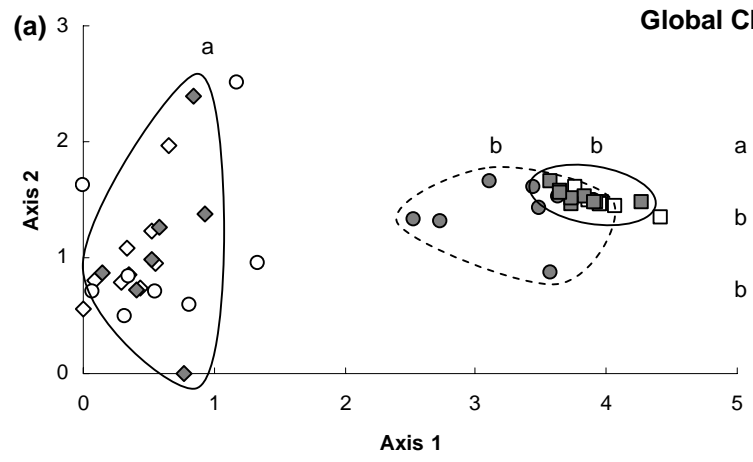
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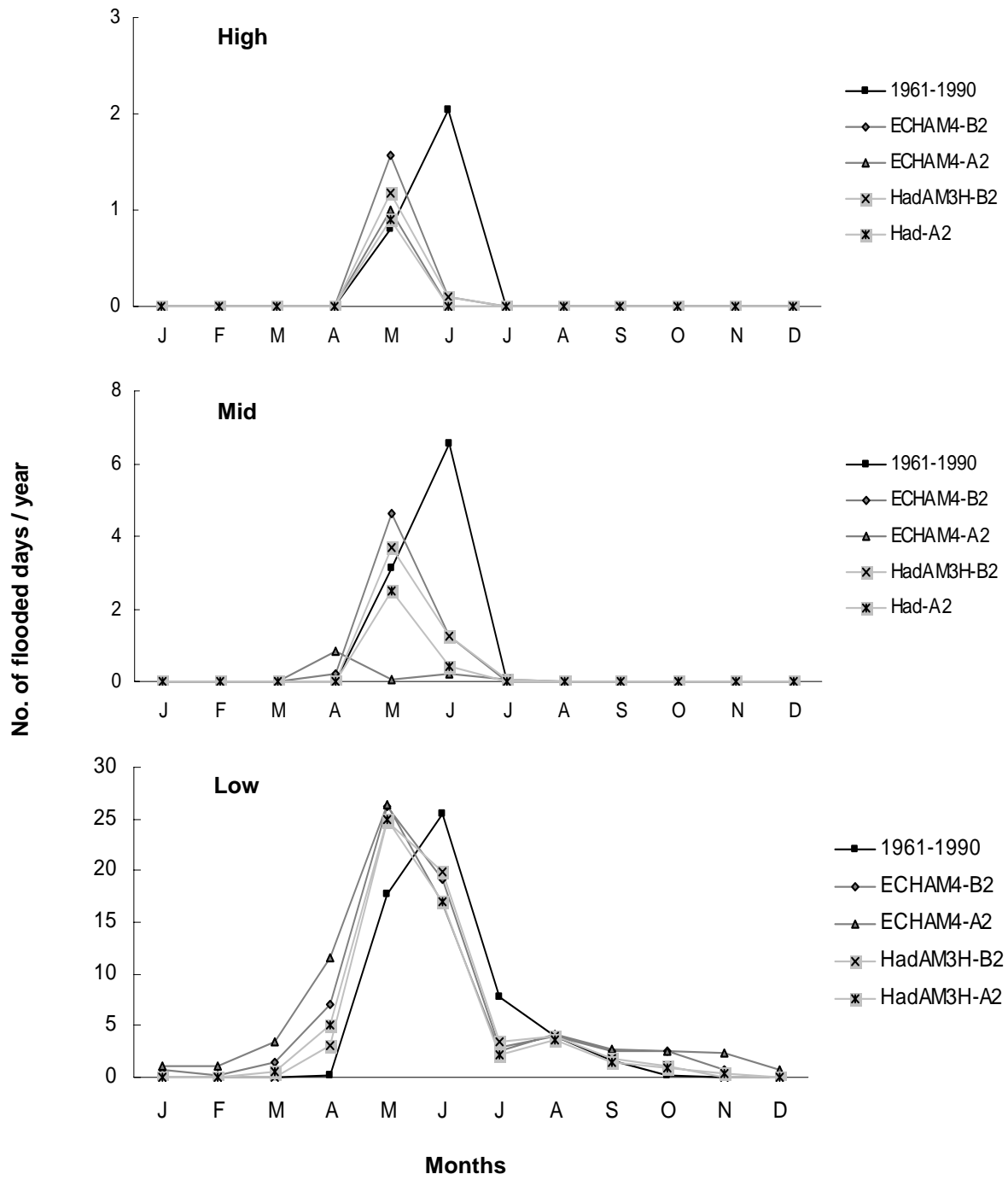


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Global Change Biology



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