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Responses of riparian trees and shrubs to flow regulation along a boreal stream in northern Sweden

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SUMMARY

1. Flow dynamics is a major determinant of riparian plant communities. Therefore, flow regulation may heavily affect riparian ecosystems. Despite the large number of dams worldwide, little specific information is available on the longitudinal impacts of dams on vegetation, for example how far downstream and at what degree of regulation a dam on a river can influence riparian woodlands.
2. We quantified the long-term responses of riparian trees and shrubs to flow regulation by identifying their lateral distribution and habitat conditions along a boreal river in northern Sweden that has been regulated by a single dam since 1948. The regulation has reduced annual flow fluctuations, this effect being largest at the dam, downstream from which it progressively decreases following the entrance of free-flowing tributaries.
3. We related changes in the distribution patterns, composition, abundance and richness of tree and shrub species to the degree of regulation along the river downstream from the dam. Regulation has triggered establishment of trees and shrubs closer to the channel, making it possible to measure ecological impacts of flow regulation as differences in vegetation attributes relative to the positions of tree and shrub communities established before and after regulation.
4. Trees and shrubs had migrated towards the mid-channel along the entire study reach, but the changes were largest immediately downstream of the dam. Shrubs were most impacted by flow regulation in terms of lateral movement, but the effect on trees extended furthest downstream.
5. The species composition of trees progressively returned to its pre-regulation state with distance downstream, but entrance of free-flowing tributaries and variation in channel morphology and substratum caused local deviations. Species richness after regulation increased for trees but decreased for shrubs. The changes in species composition and richness of trees and shrubs showed no clear downstream patterns, suggesting that other factors than the degree of regulation were more important in governing life form.

Keywords: dam, degree of regulation, ecological responses, flow regulation, northern Sweden, riparian vegetation, river, shrubs, trees

Introduction

Riparian vegetation (i.e. plants growing in the regularly flooded area along streams and rivers) is a vital component of fluvial ecosystems. It creates and stabilises fluvial habitats (Gurnell & Petts, 2002,

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2006; Corenblit *et al.*, 2007), filters hyporheic water, and influences runoff (Tabacchi *et al.*, 2000). Riparian forests provide shade, habitat, refuge and migration corridors for plants and many animals (Naiman, Décamps & Pollock, 1993; Naiman & Décamps, 1997; Salinas, Banca & Romero, 2000), including mammals and birds (Spackman & Hughes, 1995), macroinvertebrates (Aguiar, Ferreira & Pinto, 2002) and fish (Jones *et al.*, 1999; Pusey & Arthington, 2003). At a large scale, the composition, abundance and distribution of species in riparian zones and other wetlands respond to physicochemical and climatic gradients (Tabacchi *et al.*, 1996; Bernez *et al.*, 2004; Lite, Bagstad & Stromberg, 2005; Kotowski *et al.*, 2006; Sanderson, Kotliar & Steingraeber, 2008), whereas, at a small scale, the flow regime is a major governing factor (Hughes & Muller, 2003; Hughes & Rood, 2003). Flow regimes influence channel and vegetation dynamics (Molles *et al.*, 1998; Bendix & Hupp, 2000). Consequently, alteration of the flow regime results in modifications of riparian ecosystem, through impacts on vegetation, landform and habitat (Bendix & Hupp, 2000).

Previous studies have documented a range of effects of flow stabilisation on riparian communities. For example, fragmentation of riparian forests and the decline of native vegetation, and sometimes their substitution by exotic species, may accompany reduced flood disturbances below dams (Rood & Mahoney, 1990; Scott, Friedman & Auble, 1996; Rood *et al.*, 1999; Bendix & Hupp, 2000; Polzin & Rood, 2000; Cooper, Andersen & Chimner, 2003). Flow stabilisation has also been linked to shifts of post-pioneer riparian forest towards more mesoxeric formations (Bravard *et al.*, 1997; Pautou *et al.*, 1997; Merritt & Cooper, 2000; Corenblit *et al.*, 2007), and to narrowing of the main channel following encroachment by marginal vegetation (Johnson, 1994; Scott *et al.*, 1996; DeWine & Cooper, 2007). Despite much research on the effects of flow regulation, there is little specific information on how effects relate to the degree of regulation and on the extent of the effects downstream of the dam (e.g. Poff & Zimmerman, 2010). Some ideas can be inferred from studies on geomorphic effects (Ligon, Dietrich & Trush, 1995), although these may vary considerably among rivers (Williams & Wolman, 1984). In addition, the natural longitudinal changes in catchment area, channel gradient, valley shape and substratum grain size that result in distinct hydrogeomorphic processes from headwaters to lowland areas (Vannote *et al.*, 1980) have been documented to influence plant community composition and distribution within riparian zones and floodplains (Friedman *et al.*, 2006). Such changes may overlap with downstream effects of dams. Some authors have recognised the poor scientific knowledge about relationships between flow alteration and ecological communities and have highlighted the need to develop empirical models that predict ecological responses to various types and degrees of flow alteration (Bunn & Arthington, 2002; Acreman, 2005; Merritt *et al.*, 2010; Poff *et al.*, 2010). Below dams, the degree of regulation will decrease successively because of inflow from free-flowing tributaries. Boreal trees and shrubs, long-lived and sensitive to flooding (Komonen, 2009), are common in riparian zones and can therefore be used as indicators of long-term flow alteration.

The objective of this study was to analyse the ecological impact of flow regulation by comparing establishment patterns, composition, abundance and richness of riparian tree and shrub communities before and after the building of a major dam in a boreal stream, along a gradient of flow alteration at different distances downstream of the dam. Specifically we asked: (i) how far downstream of a dam can effects of regulation be identified? and (ii) how do responses of trees and shrubs vary in relation to flow regulation and other environmental factors?

Methods

Study area

The Vojm River (local name Vojmån) is a 225-km-long tributary of the Ångerman River (local name Ångermanälven) in southern Lapland (Västerbotten province, Sweden) with a catchment area of 3543.3 km^2. It originates on the western side of the mountain Kittelfjäll at 1100 m a.s.l. on the border between Sweden and Norway, flows southwest through Vojm Lake (local name Vojmsjön) and finally ends into Volg Lake (local name Volgsjön) at 350 m a.s.l. (Fig. 1; Volgsjön is not shown on map). Vojmsjön in the middle–lower part of the river was dammed and regulated in 1948 for hydropower production. The reservoir has a live storage capacity of 0.594 km^3, an 8 m vertical range of water-level and the capacity to

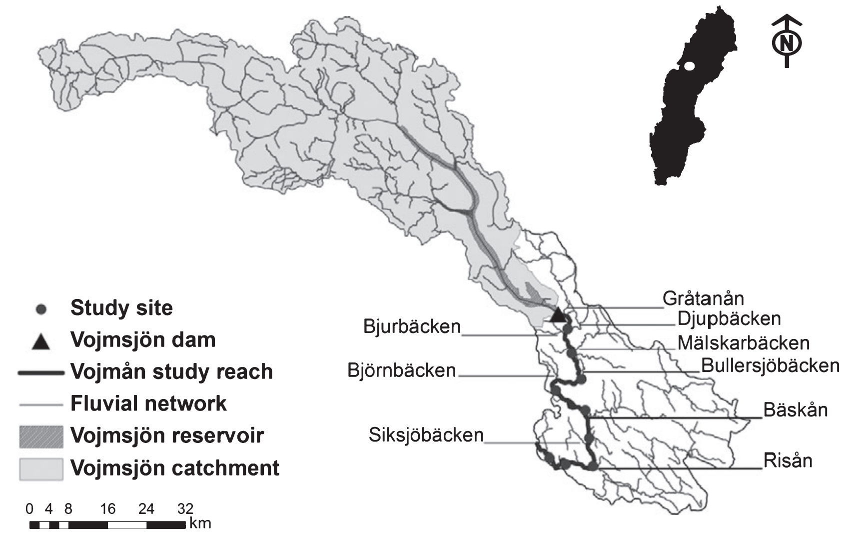

Fig. 1 Catchment of Vojmån, the location of study sites and the confluences of tributaries downstream of the Vojmsjön reservoir in northern Sweden.

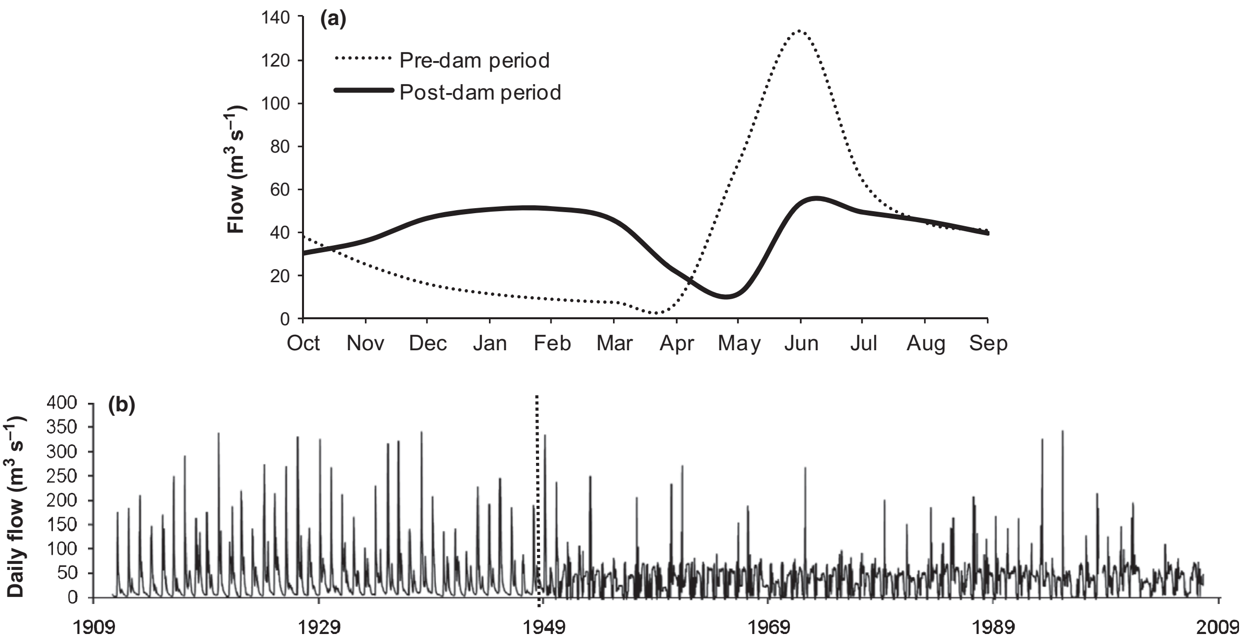

Fig. 2 Intra- (a) and inter- (b) annual flow fluctuations at the gauge (number 20033; flow series 50033) located at the dam site in Vojmsjön, northern Sweden. (a) Lines represent the mean monthly flow: the dashed line is the period before damming (pre-dam period: 1909–1947) and the solid line after damming (post-dam period: 1948–2007). (b) Line represents the mean daily flow from January 1909 to December 2007. The dashed vertical line shows the onset of flow regulation.

regulate 48% of the average total annual run-off in the basin. The catchment area upstream of the dam is 2253 km^2. Vojmån historically featured a spring flow peak with a mean daily discharge of 39 $m^3 s^{-1}$ at the site of the present dam. After damming, the flow stabilised around the annual mean throughout the year (Fig. 2a).

We studied the regulated 65-km-long reach of Vojmån between Vojmsjön and Volgsjön (Fig. 1). This is mainly a single sinuous channel, with large pools and riffles and an even gradient (mean 1.7 m km^{-1}). Vojmån receives several small (free-flowing) tributaries along this reach, its catchment growing by 1291 km^2 (Fig. 1). Among them, Bäsk River (local name Bäskån; 38 km downstream of the dam) and Ris River (local name Risån; 48 km downstream of the dam) are the largest, with catchments of 334 and

362 km^2, respectively. Flow regulation decreases from 48 to 31% before its confluence with Volgsjön (see '*Data analysis*' for an explanation of 'flow regulation'). Other pressures on the river are now slight. The solid geology along the lower Vojmån is dominated by granite and the soil consists of morainic and sedimentary deposits (Fredén, 1994). The river valley is wide and relatively flat and its native floodplain forest is dominated by *Betula pubescens* Ehrh., *Picea abies* (L.) H. Karst and *Pinus sylvestris* L. Other tree and shrub species are *Populus tremula* L., *Sorbus aucuparia* L., *Juniperus communis* L. and *Salix caprea* L. Willows are the most widespread shrubs: common species include *S. phylicifolia* L. and *S. lapponum* L.

Sampling design and field data

We were interested in the lateral extent and nature of the vegetation, along the gradient from the channel itself up into the floodplain and beyond (Fig. 3). The limit of woody riparian vegetation nearest the channel was mapped along the entire 65-km-long reach below the dam, using aerial photographs from 1947 (scale 1 : 9900 and altitude 2000 m) and modern orthophotographs from 2006 (original scale 1 : 40 000; altitude 4800 m; pixel size 0.5 m) provided by Lantmäteriet (i.e. The Swedish Mapping, Cadastral and Land Registration Authority). The 1947 aerial photographs were only available as hard copies but were digitised and georeferenced using control points from the 2006 digital aerial orthophotographs and checked with topographic maps at scale 1 : 12 500. This work was carried out using ArcGis 9.2. The reach was then divided into nine sections, each around 6.3 km long. Within each section, a 300-m-long site was selected for field survey (Fig. 1) (sites were numbered from up- to downstream). The requirements for choosing a site were as follows: (i) good access to both banks and (ii)

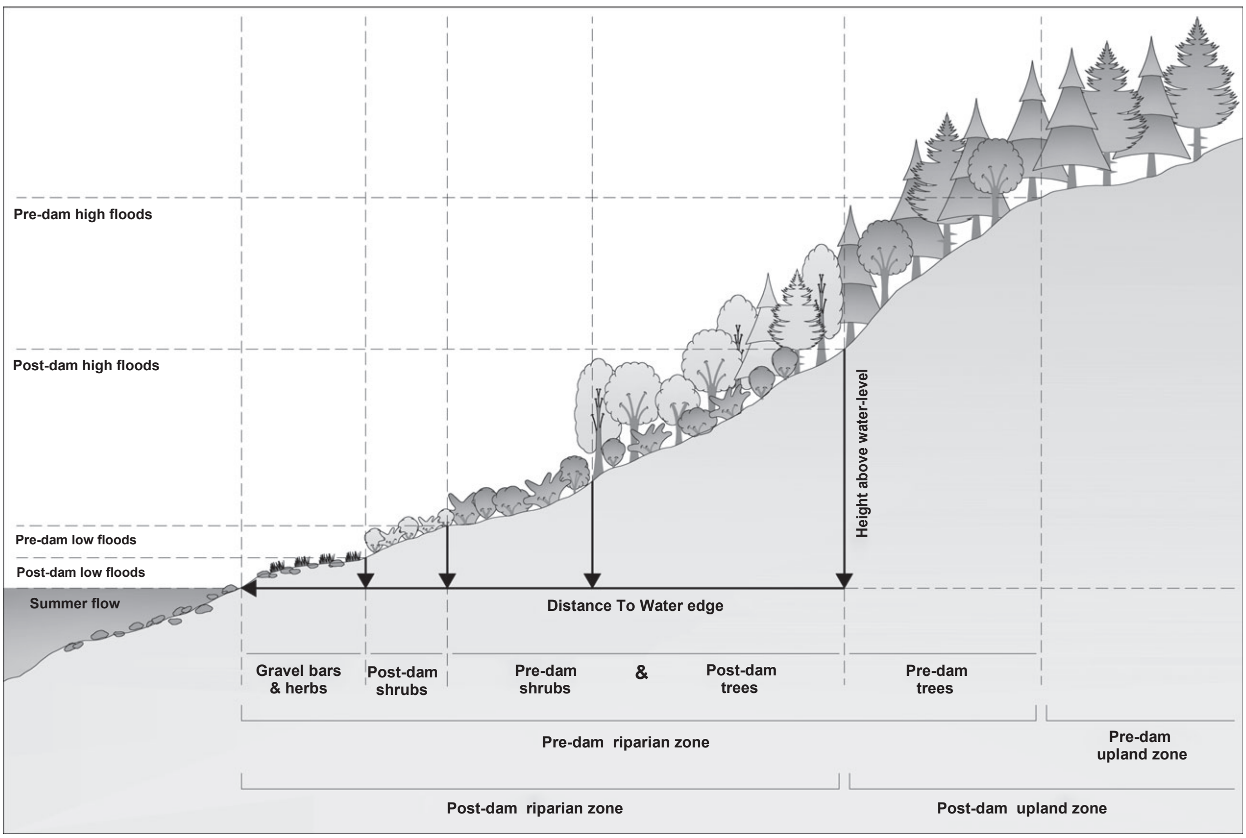

Fig. 3 Model of riparian plant distribution within the riparian zone of a regulated river. Successive and partly overlapping zones of woody vegetation reflect the pre-dam and post-dam hydrologic conditions: (i) pre-dam forest; (ii) post-dam forest; (iii) pre-dam shrubs; and (iv) post-dam shrubs. Vertical arrows represent the minimum height of the zones, and the horizontal arrow stands for the minimum distance to water edge of the zones. The terms 'low' and 'high' refer to floods with more and less frequent return periods, respectively.

no indications of any disturbance other than flow regulation. At each selected site, surveys were carried out along four 30-m wide transects 50 m apart perpendicular to the main channel.

Within each transect (and on each side of the river), the following successive and partly overlapping zones of woody vegetation were distinguished, up- to downslope: (i) pre-dam forest; (ii) post-dam forest; (iii) pre-dam shrubs; and (iv) post-dam shrubs (Fig. 3). Woody plants >2 m were considered as trees and those between 0.3 and 2 m as shrubs (Kullman, 1979; Egger *et al*., 2007). Individuals <0.3 m were not taken into account, thus avoiding small plants that would not integrate long enough periods to be useful as indicators of change in flow variation. The pre-dam vegetation (i.e. established before the dam was closed) consisted of mature trees and shrubs and in the field differed clearly from post-dam vegetation, which consisted of considerably younger individuals (<60 years). Since different tree and shrub species have specific water requirements and sensitivities to flood disturbance, and because shrubs usually grow closer to the water than trees (Ward *et al*., 2002), we hypothesized that their position relative to the water's edge should follow a consistent pattern (Fig. 3). Such zonation is very distinct along rivers governed by a spring flood regime (Nilsson, 1999).

At each site, we recorded a number of biological and physical variables. We assessed hydraulic conditions by classifying sites as pools or riffles and noted whether there was net erosion or aggradation of the banks or other types of disturbance. Within each transect, we classified the slope of the bank as low (<3.5%), gently sloping (3.5–10%), moderate (10–25%) and steep (>25%). The calibre of substratum particles in the riparian zone (the 0- to 20-cm-deep layer in which woody plants are rooted) was assessed by eye following the Wentworth scale, adding bedrock and peat (following Nilsson *et al*., 1994). To rank substrata in terms of water-holding capacity, a value of substratum fineness was weighted by the percentage composition of the riverbank substrata and based on nine Φ (phi) values ($\log_2$ transformation of the size classification): peat (−12), clay (−9.0), silt (−6.5), sand (−2.0), gravel (2.0), pebbles (4.5), cobbles (6.5), boulders (9.0) and bedrock (12) (Wright *et al*., 1984; Nilsson *et al*., 1989). Finally, for each vegetation zone we identified the different woody species, evaluated their relative abundance and measured the distance to the water's edge and the height above water level (both in summer) from the lowest limit of each vegetation zone. Field surveys were carried out in August 2009. Measurements were made by using a Suunto level, a measuring tape and a laser distance measuring tool.

Data analysis

Mean daily discharge data at the present Vojmsjön dam site (gauge 20031; discharge series 50033; provided by the Swedish Meteorological and Hydrological Institute) were used to characterise hydrologic changes over a continuous record since 1909. We analysed the free-flowing (1909–1947) and regulated (1948–2008) periods for total annual discharge, mean monthly flow, flood frequency, minimum and maximum flows within periods of 1, 3, 7, 30 and 90 consecutive days, and the rate of change. Some of these variables were obtained from the IHA (indicators of Hydrologic Alteration) computer program (Richter *et al*., 1996). We obtained a flood frequency curve by fitting a Gumbel distribution function to the series of daily maximum flows. The effect of the dam on floods was estimated as the ratio between the regulated and free-flowing values (Schmidt & Wilcock, 2008) for flows corresponding to the following return periods: T2 (i.e. every 2 years), T4, T5, T10, T25, T50 and T100. To quantify hydrologic impact along the reach downstream of the dam, we calculated the degree of regulation as the percent of the natural mean annual runoff that could be stored in the reservoir (Batalla, Gómez & Kondolf, 2004).

We tested for differences between pre-dam and post-dam establishment of woody plants by comparing distance to and height above the summer water-level (as of August 2009) for trees and shrubs within each study site. Based on Naiman & Décamps (1997), the areal reduction in the riparian zone (i.e. consequent upon regulation) was calculated for each site by measuring the migration of the riparian forest zone relative to the water-edge and multiplying by 300 m (site length) and two river banks. To compare changes in the establishment of riparian trees and shrubs among the nine study sites after the dam was closed, changes in distribution were standardised by using the ratio between the post-dam and pre-dam locations of trees and shrubs. The resulting value was termed a Distance Recovery Index (DRI, i.e. the distance over the ground to the water's edge in summer of vegetation established after the dam, divided by the distance to the water's edge of vegetation established before the dam) and Height Recovery Index (HRI, i.e. height above the water level of vegetation established after the dam, divided by height of vegetation established before the dam). 'Recovery' stands for recovery from the regulation effect. Thus, when there is no effect of regulation, indices are equal to or exceed one and vegetation attributes have returned to pre-regulation conditions. The longitudinal trends of change in lateral distance and height were analysed through simple regression analyses of all DRI and HRI values per site, with degree of regulation as the independent variable. A few other factors that could attenuate or exacerbate the effects of regulation on woody plant establishment were also analysed. We compared all DRI and HRI values from the study sites upstream (sites 1–5) and downstream (sites 6–9) from the confluence with Bäskån (the first large tributary below the dam), which represents a shift in substratum grain size, and tested for differences in DRI and HRI values among categories of bank topography. Tests for significant differences were carried out using analysis of variance (one-way ANOVA).

We used Detrended Correspondence Analysis (DCA; CANOCO 4.5; Ter Braak & Smilauer, 1998) to evaluate regulation effects by comparing the species composition of trees and shrubs established before and after dam closure. Multiple regression among DCA axes and environmental variables was used to assess how environmental variables influenced species responses. In order to improve the ordination trends, rare species were downweighted. The effects of regulation on species composition were indicated by Sørensen's index of similarity (Kent & Coker, 1996). The total number of tree and shrub species at each site was recorded and divided by the natural logarithm of its area to allow unbiased comparisons. Differences between standardised species numbers established before and after dam closure were tested using one-way ANOVA.

Results

Hydrological alteration

Not surprisingly, the mean annual runoff in Vojmån was almost identical between the free-flowing (1246 hm^3 $year^{-1}$; 1909–1947) and regulated (1225

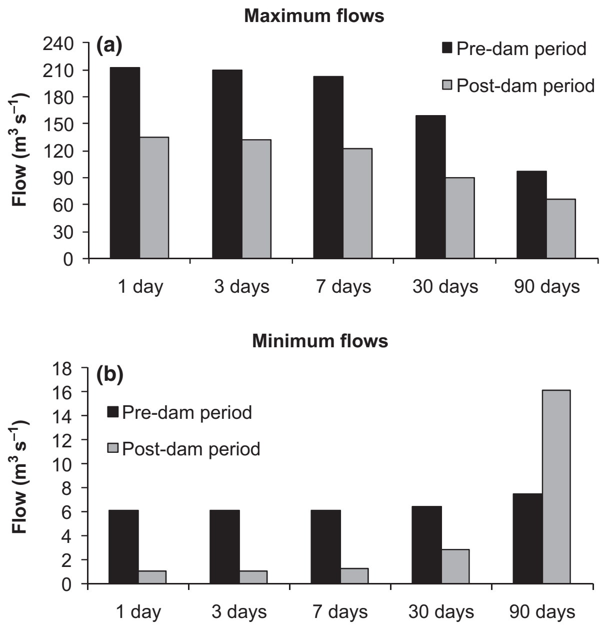

Fig. 4 Average flows during periods of 1–90 consecutive days for the pre- (1909–1947) and post-dam (1948–2007) periods at the gauging station number 20033 (flow series 50033) located at the dam site in Vojmsjön, northern Sweden. Values have been calculated using IHA software (Indicators of Hydrologic Alteration; Richter *et al.*, 1996).

hm^3 $year^{-1}$; 1948–2008) periods, but the fluctuation in discharge within years decreased (Fig. 2a). The regulated flow regime is almost opposite to the natural one, being higher during autumn and winter and lower during spring and summer. Maximum flows have decreased by around 50% and minimum flows have increased when averaged over 90 consecutive days (Fig. 4). However, the dam is almost closed for about 17 days $year^{-1}$, implying that the minimum flows over a 30-day period have decreased by >80%. Flood events have also been reduced (Fig. 2b). For example, flood magnitudes after regulation (T2 to T100) ranged between 0.58 and 0.86 times the natural values (Table 1). The highest reduction occurred for floods returning every second year (T2), which decreased from 206 to 120 m^3 s^{-1} after the dam was closed. Finally, the rate of change – calculated using the IHA program with daily data – increased by 20 and 40%, respectively, after regulation. Downstream from the dam, the degree of regulation decreased from 49% at the dam site to 30% 65 km further downstream, where the river enters a major, heavily regulated river (Supporting information, Appendixes S1 and S2).

Table 1 Discharge magnitudes (Q) calculated by fitting a Gumbel distribution function to the series of daily maximum flows for the pre-dam (Q_{nat}; 1909–1947) and post-dam (Q_{reg}; 1948–2007) periods

Return period (years)	Natural flow ($m^3\ s^{-1}$)	Regulated flow ($m^3\ s^{-1}$)	Q_{reg}/Q_{nat}
2	206	120	0.58
4	254	175	0.69
5	267	190	0.71
10	309	236	0.76
25	362	293	0.81
50	401	336	0.84
100	439	378	0.86
200	478	420	0.88

Changes in physical variables

The type of bank substratum was the only variable that varied with position downstream. Study sites 1–5 upstream of Bäskån had significantly coarser substrata ($P < 0.05$) than sites 6–9 downstream (median values of weighted substratum fineness were 3.2 and −8.2, respectively).

Changes in establishment patterns of woody vegetation

The aerial photographs from 2006 showed that the woody riparian vegetation had advanced towards the main channel along the entire reach downstream from the dam. These results laid the basis for selection of sites for more detailed study. An ANOVA test on pre- and post-dam distances and heights of tree and shrub positions relative to the watered channel showed a significant advance of trees and shrubs towards the channel after the dam was closed (Supporting information, Appendix S3). On average, trees were 3.8 m closer to the channel, whereas shrubs grew 1 m closer (Appendix S3). In terms of height, trees grew 0.4 m and shrubs 0.2 m lower than before the dam was closed (Appendix S3). The largest changes were found directly below the dam (Appendix S3). The riparian zone experienced a 45% areal reduction after damming, from a mean of 5360 m^2 to 3000 m^2 per 300-m along the river (including both banks). The reduction in riparian area varied from a mean of 62% for the first four study sites downstream of the dam to 31% for the last five sites.

The DRI and HRI values varied between 0 and 1 at the study sites (Fig. 5). Although higher values are possible, values >1 were not found. The lowest DRI and HRI values occurred close to the dam, i.e. the migration of vegetation towards the channel was most pronounced where the degree of regulation exceeded 40%. Trees and shrubs had different response curves; a polynomial function for trees and a linear for shrubs (Fig. 5). Values of r^2 were high for HRI indices ($r^2 = 0.56$; $P = <0.0001$ for trees; $r^2 = 0.69$; $P = <0.0001$ for shrubs) and lower for DRI indices ($r^2 = 0.17$; $P = <0.001$ for trees; $r^2 = <0.54$; $P = <0.0001$ for shrubs). Among sites located upstream of the first major tributary, only banks with coarse substratum ($\Phi > 9.0$; boulders and bedrock) failed to show establishment changes for trees after regulation (DRI and HRI = 1; Fig. 5 and Appendix S4). Similarly, tree establishment changes within steep banks were low (Figs 5 & 6).

Changes in woody species composition and richness

The mean number of species was generally higher among riparian trees established after the dam was closed (1.31 compared to 0.89 species/ln area; $P < 0.05$), but the mean number of shrub species decreased after regulation (from 0.91 to 0.77 species/ln area; $P < 0.05$; Fig. 7). The species richness of trees and shrubs did not show any clear downstream patterns. The floristic similarity (Sørensen's index) between the floras established before and after regulation varied between 0.72 and 0.90 for trees, and between 0.57 and 0.67 for shrubs. Sites located downstream of the first major tributary presented significantly higher similarity values for the pre- and post-dam tree floras than did sites upstream ($P < 0.05$), whereas similarity for the corresponding shrub floras did not vary with position downstream ($P > 0.05$).

The DCA separated tree species along the first two axes [eigenvalue (λ) axis 1 = 0.36; axis 2 = 0.15], and together they explained 56% of the total variation (Fig. 8a). These axes were well correlated with environmental variables ($r = 0.63$). The first axis was positively related to height and distance for the position of trees and negatively to the degree of regulation (Fig. 8b). Trees established after dam closure were positioned on the left side of the diagram and dominant species included *Alnus incana* L. Moench, *Prunus padus* L. and *Salix caprea* (Fig. 8a). Trees established before dam closure were located on

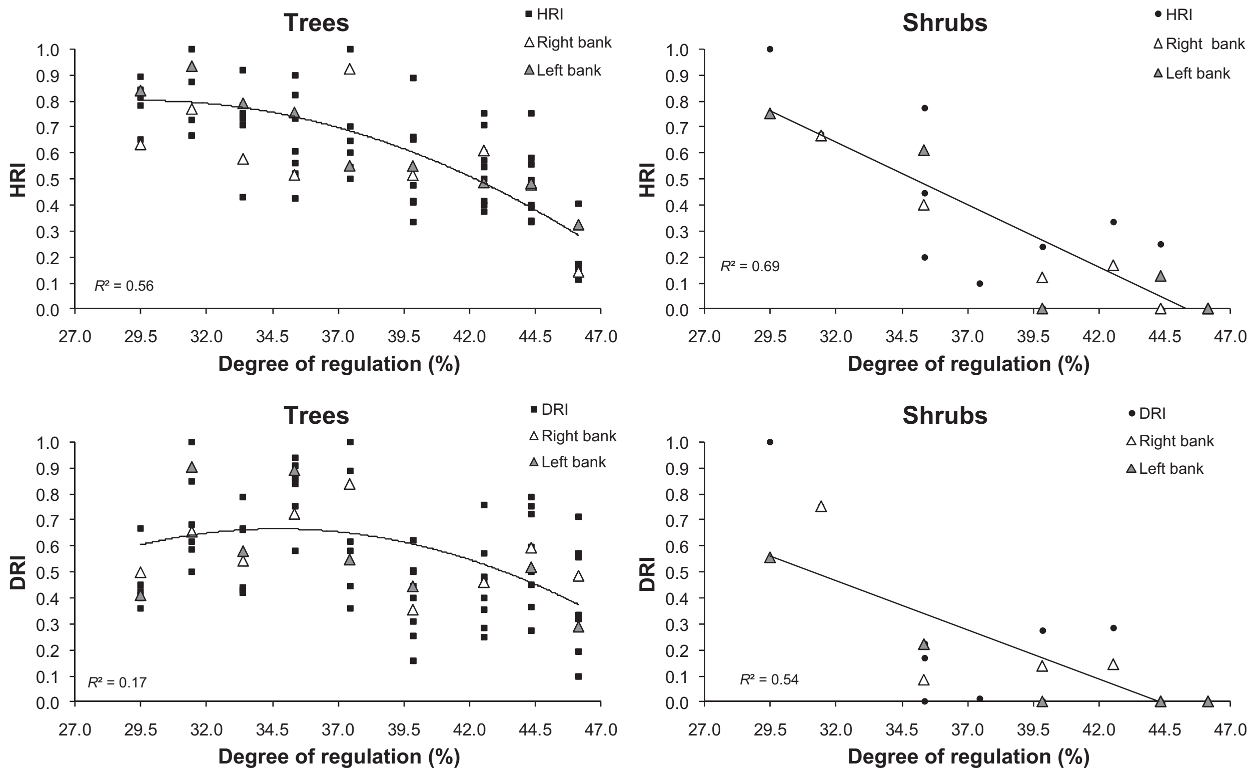

Fig. 5 Height Recovery Index (HRI) and Distance Recovery Index (DRI) for trees and shrubs against the degree of regulation. Squares and dots represent the HRI and DRI values in the nine study sites for trees and shrubs, respectively. Triangles represent mean HRI and DRI values per bank (left and right). 0 represents the largest change, whereas 1 means no change. Regression lines show the relationships between establishment changes and the degree of regulation along the entire study reach downstream of the dam. $P < 0.0001$ for the HRI for trees and shrubs and the DRI for shrubs, and $P < 0.001$ for the DRI for trees.

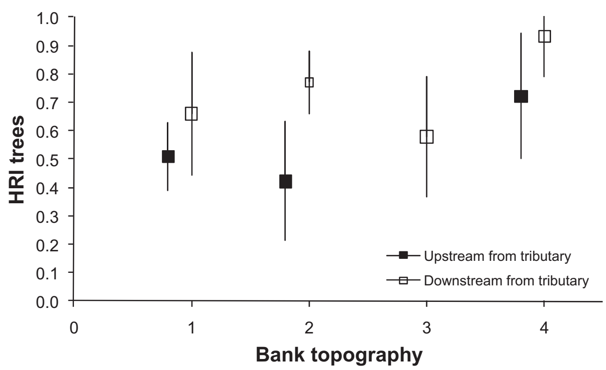

Fig. 6 Mean and standard deviation of the Height Recovery Index for trees for the four bank topography categories described at the sampled sites: (1) low flat banks (<3.5%); (2) gently sloping banks (3.5%–10%); (3) moderately banks (10%–25%); and (4) steep banks (>25%). 'Upstream tributary' and 'downstream tributary' refer to the average values for sites 1–5 and sites 6–9, upstream and downstream, respectively, of the first major tributary (Bäskån).

the right side of the diagram, and the most frequent were *Populus tremula*, *Pinus sylvestris* and *Sorbus aucuparia*. On the first axis, communities ranged from trees growing in low areas of the riparian zone close to the dam to communities dominated by trees growing in higher areas further downstream. The second axis was correlated with substratum characteristics – most strongly with the proportion of bedrock – with a correlation coefficient of 0.56. Only trees established before dam closure responded to substratum (Fig. 8b). *Betula pubescens*, *Picea abies* and *Juniperus communis* were represented in the centre of the diagram (Fig. 8a).

The eigenvalues for shrub species on the first two DCA ordination axes were 0.22 and 0.1, respectively, and together they explained 37.8% of the total variation of shrubs (Fig. 8c). The separation of shrubs in relation to the time of establishment was weaker than for trees. Young specimens of *Alnus incana*, *Rosa*

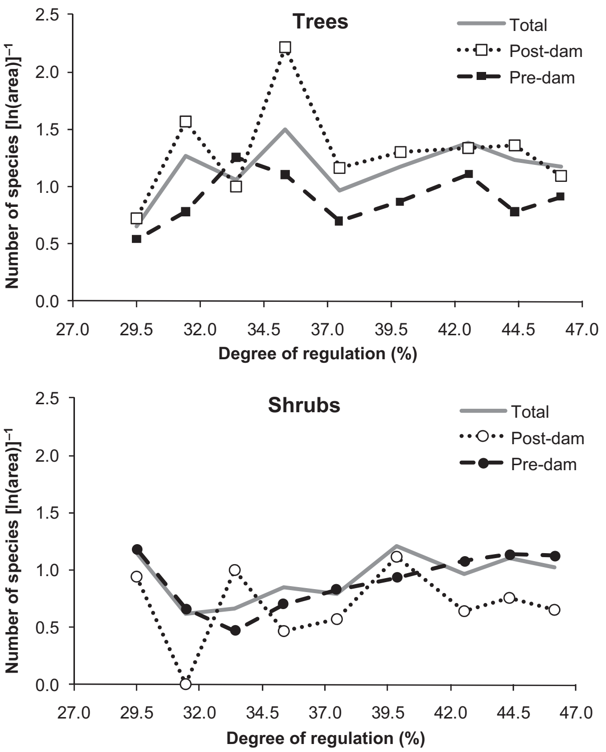

Fig. 7 The number of tree and shrub species in pre- and post-dam communities and in total in relation to the degree of regulation per site. The Y axis shows the number of species divided by ln area.

majalis Herrm., *Salix pentandra* L. and *Ribes spicatum* E. Robson appeared on the right side of the DCA diagram, while *Juniperus communis*, *Salix starkeana* Willd., young specimens of *S. caprea* and *Betula nana* L. were located on the left and were commonly part of shrub communities established after dam closure. The effect of the second axis was more important for shrubs established after dam closure. *Salix triandra* L., *S. lapponum* and *S. phylicifolia* did not occupy clear positions on the DCA diagram (Fig. 8c). The correlation between environmental variables and axes showed that shrub species related mainly to the type of substratum (Fig. 8d). Other physical variables that contributed significantly to shrub species distribution were bank topography and water turbulence. The DCA ordination on the first axis distinguished shrubs growing on pebble deposits from shrubs growing on clay. The coefficient for the correlation between species and environmental variables was 0.42. The second axis distinguished between shrubs on sand and cobbles (Fig. 8d) and also contained information about bank topography. The coefficient for the correlation between species and environmental variables was 0.44.

Discussion

After the building of the dam at Vojmsjön, flow downstream of the reservoir stabilised (Figs 2 & 4), although with increased small-scale fluctuations. This has resulted in a halving of the original riparian area and in a large expansion of trees and shrubs towards the channel (Fig. 5; Appendix S3). This vegetation encroachment corroborates results of similar studies elsewhere of local vegetation responses to reduced flooding (Johnson *et al.*, 1995; Scott *et al.*, 1996; Scott, Auble & Friedman, 1997; Merritt & Cooper, 2000; Cooper *et al.*, 2003; Birken & Cooper, 2006; DeWine & Cooper, 2007). Other investigations have pointed out the importance of periodic floods for increasing the number of potential regeneration sites, the delivery and establishment of seeds, and the vegetative regeneration processes, through channel movement, and supply of water, sediment and organic debris (Johnson, Burgess & Keammerer, 1976; Poff *et al.*, 1997; Molles *et al.*, 1998; Bendix & Hupp, 2000; Hughes & Muller, 2003). Despite regulation and its probable effects on such processes, our results do not indicate any substantial reduction in the availability of propagules, suggesting the existence of a riparian seed bank, seed rain from the adjacent uplands or that hydrochorous dispersal of seeds remains effective (Nilsson, Gardfjell & Grelsson, 1991; Nilsson *et al.*, 2010). On the other hand, the substantial decrease in major floods (from 2 to 4 times to less than once every 100 years) explains the lateral hydrologic disconnection of the distal pre-regulation riparian forest and its likely gradual development into upland forest.

We identified a downstream change in plant establishment that corresponded to a decrease in the degree of flow regulation, following the confluence with more free-flowing water as the catchment area increased (Fig. 5). Recent studies (Acreman & Dunbar, 2004; Acreman, 2005; Poff & Zimmerman, 2010; Poff *et al.*, 2010) have pointed to the need for such data. The largest encroachment of vegetation was found in the four study sites closest to the dam, corresponding to a degree of regulation >40%. An extrapolation of response curves (Fig. 5) suggests that some vegetation variables (i.e. position of trees) would remain displaced until the degree of regulation equalled

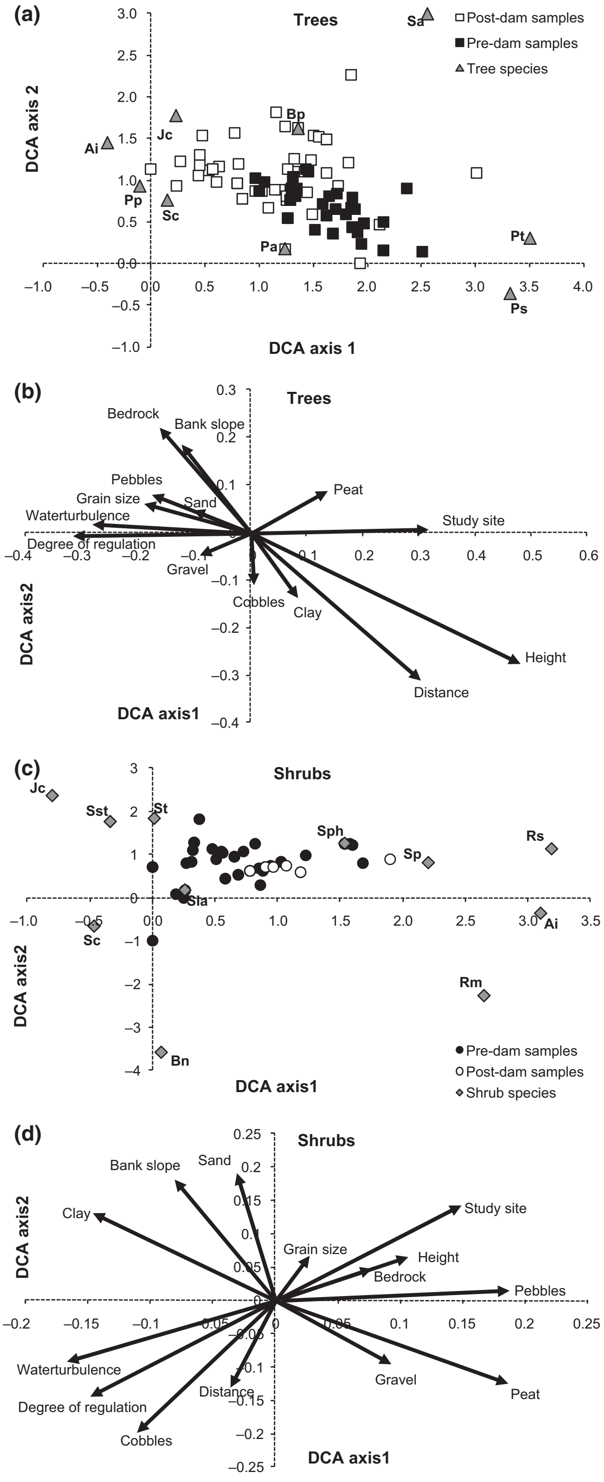

Fig. 8 Detrended Correspondence Analysis diagrams. Diagrams (a) and (c) represent the first two axes of the DCA using species composition in the sampled vegetation bands. Filled symbols represent pre-dam and unfilled symbols represent post-dam zones of trees and shrubs. Diagrams (b) and (d) show results from the multiple regression between the first two DCA axes and the measured environmental variables for trees and shrubs. The length of arrows indicates the relative importance of the environmental variable, and the axis units are correlation coefficients, indicating the relationship between the variable and the corresponding axis. Sa: *Sorbus aucuparia* L.; Ps: *Pinus sylvestris* L.; Pt: *Populus tremula* L.; Pa: *Picea abies* (L.) H. Karst; Bp: *Betula pubescens* Ehrh.; Jc: *Juniperus communis* L.; Sc: *Salix caprea* L.; Pp: *Prunus padus* L.; Ai: *Alnus incana* L. Moench; Bn: *Betula nana* L.; Sst: *Salix starkeana* Willd.; St: *Salix triandra* L.; Sla: *Salix lapponum* L.; Sph: *Salix phylicifolia* L.; Sp: *Salix pentandra* L.; Rm: *Rosa majalis* Herrm.; Rs: *Ribes spicatum* E. Robson.

23–26%, which in Vojmån would be up to 80–95 km downstream of the dam (i.e. exceeding the actual length of the river). According to their catchment areas, the Bäskån and Risån tributaries contribute 26% (185 hm^3 $year^{-1}$) and 28% (200 hm^3 $year^{-1}$), respectively, of the total runoff from the study area (702 hm^3 $year^{-1}$). This means that they reduce the degree of regulation by 4.5 and 3.7%, respectively, which is more than for any other tributary (Appendix S2). Furthermore, our substratum measurements show that the material in the main channel is coarser closer to the dam upstream of these confluences and much finer downstream of the confluences. This could partly be because of the fact that the water is 'hungry' and more erosive after release from the reservoir (Kondolf, 1997). Resultant downcutting processes would be offset by replenishment of finer substrata from free-flowing tributaries. In general, rivers often undergo geomorphological adaptations below tributary confluences (Petts, 1979; Williams & Wolman, 1984; Chien, 1985; Schmidt & Wilcock, 2008), leading to increases in habitat heterogeneity, biological diversity and productivity in riverine ecosystems (Benda *et al.*, 2004). Thus, water and sediment supply from tributaries could enhance the recovery of hydrogeomorphological and vegetation conditions. In addition to the flow, bank topography and substratum are also important in controlling vegetation responses to regulation. Limited vegetation encroachment on the steep banks of Vojmån can be explained by the small area affected by flow changes, and partly also by the coarse substratum at such sites (Fig. 6). By contrast, almost flat riparian sites with fine sediments provide ideal conditions for observing even small changes in vegetation establishment. According to our results, the ground height of woody plants reflects hydrologic alteration better than their distance to the water level. The fact that downstream responses differed between trees and shrubs is probably related to their different locations within the riparian zone. These are conditioned mainly by the balance between water requirements and resistance to flood disturbance and anoxia (Glenz *et al*., 2006). The flexible stems and re-sprouting ability of shrubs also allow them to colonise areas closer to the active channel.

The ordination of environmental variables shows that physical variables, such as substratum, water turbulence and bank shape, can be even more important than flow regulation in conditioning the species composition of new shrub communities. However, the degree of regulation (and hence distance from the dam) was the major variable governing the species composition of trees (Fig. 8). Although species composition of trees differed between those that had established before and after the dam was closed, species were still recruited from the local flora. In many rivers, invasion of floodplains by non-native species after regulation is a major ecological issue, e.g. *Tamarix* in the western United States (Sher, Marshall & Gilbert, 2000; Birken & Cooper, 2006; Merritt & Poff, 2010). Vojmån did not have any exotic trees or shrubs that had colonised after regulation, however (cf. Dynesius *et al*., 2004). The fact that the tree communities established before and after the dam was closed showed an increasing floristic similarity downstream of the mouth of the first major tributary supports the hypothesis of a 'healing' effect of tributaries. By contrast, the fact that the shrubs lacked such patterns is consistent with the hypothesis of local conditioning factors, such as substratum type. Lower rooting depth of shrubs, erosion of banks below the dam, increased flows during winter and ice formation over a larger area, all affect the survival of shrub saplings more than they affect young trees, since the colonisation areas for shrubs are typically closer to the active channel (Nilsson, 1999). Obviously, plant species richness along fluvial corridors can be governed by other factors in addition to flow, such as fluvial geomorphic landforms, river size and biotic variables (Tabacchi *et al*., 1996; Pollock, Naiman & Hanley, 1998). For example, Merritt & Cooper (2000) and Merritt & Wohl (2006) did not find differences in species richness between flow-regulated and free-flowing reaches.

In conclusion, flow regulation is an important driver of geomorphological and ecological reorganisation of riparian zones. The native riparian tree and shrub species remain, but after the dam was closed the individuals established at lower heights. Our finding that a single dam can affect biota far downstream is important and has implications for the assessment of regulation effects worldwide. Given that a majority of the world's rivers are regulated by dams (Nilsson *et al*., 2005), their ecological effects might be more far-reaching than has been previously appreciated. In addition, our findings could assist in the identification and delimitation of rivers significantly affected by hydrologic alteration (European Commission, 2000) and contribute to the prediction of future changes in riverine ecosystems, since regulated rivers provide hydrologic conditions analogous to the flow scenarios envisaged for instance for northern Europe following future global warming (Hultine *et al*., 2007). Finally, the defined quantitative relationships between flow alteration and vegetation responses improve the basis for adaptive management, which will support stakeholders when defining ecosystem management goals, particularly for the design of environmental flows (Arthington *et al*., 2010).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Gradient of hydrologic alteration along the 65 km study reach of Vojmån measured as the degree of regulation (defined as the percentage of the mean annual discharge that can be stored in upstream reservoirs).

Appendix S2. Data showing the decrease in the degree of regulation (see Appendix S1 for definition) in Vojmån at various points downstream of the Vojmsjön dam.

Appendix S3. Mean and standard deviation of the height (vertical distance from stream) and distance (lateral distance from stream) for established trees and shrubs on the riparian study sites.

Appendix S4. Changes in the establishment patterns of trees (expressed as Height Recovery Index, HRI) against bank substratum fineness (weighted by percentage composition of the riverbank substratum and based on nine Φ values).

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