Effects of restoration on riparian biodiversity in secondary channels of the Pite River

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Abstract
Rivers throughout northern Sweden have been channelised for timber floating. Floatway constructions and modifications have resulted in simplified channel morphologies and flow regimes, affecting the habitat of aquatic invertebrates, fish communities and vegetation in the riparian zone. In recent years, some rivers used for log transportation have been restored. In general, restoration is expected to create more heterogeneous flow regimes and patterns of fluvial disturbance. Recent studies suggest that such restoration may result in altered species composition and enhanced species richness in riparian plant communities. This study examines the effects of restoration on riparian vegetation communities adjacent to secondary channels that have been cut off by floatway constructions in the Pite River watershed. Surveys of riparian plant communities at channelised and restored sites indicate that species richness and evenness are not higher at restored sites compared to channelised sites. Although the results do not show the predicted effects of restoration on species richness, there are differences in species composition. Principal components analysis suggests that plots closest to the river at channelised sites comprise a distinct community with relatively high abundances of moisture-tolerant species, whereas plots at restored sites are more typical of dryer, upland forests. These findings suggest an upland shift in the location of the riparian zone following restoration, as floodplain habitats that were exposed by lower water levels during the period of channelisation were submerged following the re-opening of side channels. These results suggest that riparian plant communities in the Pite River watershed may require more than five years to recover and adapt to post-restoration conditions.

Sammanfattning
Introduction

The rivers of northern Sweden played a very important role in Sweden's industrialisation. As the need for timber rose in Western Europe, the forest industry started to use rivers for transporting timber from inland forests down to the sawmills on the coast. In northern Sweden this activity started around the 1850s and went on until the 1970s (Törnlund and Östlund, 2002). To facilitate log transportation, rivers were channelised: Structures such as stone piers were built to line river banks and cut off secondary channels and meander bends, and the rivers were cleared of boulders and large woody debris. These constructions and modifications resulted in simplified channel morphologies and flow regimes (Muotka and Laasonen 2002), affecting the habitat of aquatic invertebrates and fish communities (Huusko and Yrjänä 1997), as well as the vegetation in the riparian zone (Capon et al. manuscript in preparation).

The riparian zone is of great importance in the landscape, being a transition zone between aquatic and terrestrial ecosystems (Nilsson et al. 1994; Nilsson and Svedmark 2002) encompassing sharp environmental gradients in ecological processes and communities (Naiman et al. 1993). The flow regime is the dominant factor in structuring riparian ecosystems, as spatial and temporal changes in river flow create heterogeneous environments and contribute to the redistribution of organic and inorganic matter in the riparian zone (Nilsson and Svedmark 2002).

Riparian zones often have high species richness compared to their surroundings (Naiman et al. 1993). This is due in large part to the fact that riparian zones tend to experience more frequent disturbances than do surrounding upland habitats. Riparian zones are strongly influenced by fluvial disturbance such as flooding, sediment deposition and lateral channel migration, which results in temporally and spatially heterogeneous substrates (Naiman et al. 1993, Nilsson and Jansson 1995). Because of their low-lying position within the watershed, riparian corridors are also influenced by colluvial disturbance events imposed by upland environments (Nilsson and Svedmark 2002). The intermediate disturbance hypothesis (Connel 1978, Huston 1994) predicts that the highest levels of species diversity will tend to occur at intermediate levels of disturbance frequency and intensity (Huston 1994). In riparian ecosystems, the most species rich communities can be found in places with intermediate levels of flood frequency and high levels of spatial variation in flood frequency (Pollock et al. 1998). Frequent, low-intensity floods limit competitive exclusion by dominant species and create open patches for colonisation by opportunistic species (Nilsson and Grelsson 1990). In contrast, infrequent floods of high intensity or duration may denude large areas of riparian vegetation by dislodging or burying plants (Bendix 1999), or by creating anaerobic soil conditions (Blom and Voesenek 1996, Friedman and Auble 1999).

Another factor contributing to the species richness of riparian plant communities is their ability to use the river as means of dispersal. The propagules of most riparian plants can be dispersed by water (i.e., hydrochory), although their floating capacities may vary (Andersson et al. 2000).

Channelisation associated with timber floating in Sweden has altered the structure and dynamics of the riparian ecosystem and river-riparian interactions, creating new conditions for the riparian systems. At the watershed scale, channelisation reduces sinuosity and the total length of the riparian ecotone, which limits land-water interactions. At the reach scale, channelisation alters the flood regime leading to decreased flood frequency (Nilsson et al. 2005), decreased lateral (i.e., aquatic - riparian) movement of drift
material (Andersson et al. 2000) and declining rates of litter decomposition (Ellis et al. 1999). Channelisation also decreases substrate heterogeneity and variability of stream flow (Nilsson et al. 2005) and reduces retention efficiency of detritus, since retentive structures such as debris dams, back-waters and boulders are removed (Muotka and Laasonen 2002). As a result, the creation of new habitat suitable for plant recruitment is reduced (Goodwin et al. 1997), and riparian areas become less biologically active (Nilsson and Svedmark 2002). In large rivers, tributaries and cut-off secondary channels, channelisation generally results in less frequent but more intense flooding, as floatway constructions function as artificial levees shielding the riparian zone from all but the most infrequent, catastrophic floods (Nilsson et al. 2005). Cut-off side channels are further impacted by reduced water levels and in some case even drying, which can lead to expansion of the forest towards the waterline (Nilsson and Svedmark 2002).

In recent years, some of the rivers that have been affected by timber floating have been restored. Objectives of restoration are mainly focused on improving habitat for fish, particularly Salmo salar and Salmo trutta. By removing floatway constructions that cut off secondary channels, channel complexity is restored and new aquatic habitats are re-opened. In general, restoration is expected to create more heterogeneous flow regimes and patterns of fluvial disturbance (Nilsson et al. 2005). Accordingly, these changes affect not only aquatic ecosystems but also riparian vegetation.

A recent study of tributaries used for timber floating in the Vindel River, Sweden (Capon et al. manuscript in preparation) demonstrated that species richness and evenness of riparian plants was significantly higher at restored sites relative to channelised sites. This trend was evident in plots up to 15 m from the edge of the stream, although the greatest difference between channelised and restored sites in species richness was at intermediate distances from the channel’s edge (i.e., 1-2 m, 2-3 m, and 4-5m). These findings suggest that such restoration may result in an altered species composition and enhanced species richness in riparian plant communities (Capon et al. manuscript in preparation).

Whereas the Vindel River study investigated the effects of restoration in tributaries, comparatively little is known about the effects of restoration in secondary channels. In this study I have examined the effects of restoration on riparian vegetation adjacent to secondary channels that have been cut off by floatway constructions. The objectives of this study are to compare the species richness and composition of vascular plant communities at channelised and restored sites in the Pite River watershed. I predicted that, after restoration, the re-opening would lead to an increase in flow that would create more heterogeneous flood disturbance regimes, thereby enhancing the diversity of riparian plants.

Methods
Study sites
The study was conducted in the Pite River watershed, in the boreal region of northern Sweden (Fig. 1). Upland vegetation in this region is predominantly dry to mesic managed forest dominated by Pinus sylvestris and Picea abies with an understory of dwarf shrubs such as Vaccinium spp. and Empetrum hermaphroditum as well as mosses and lichens (J. Engström personal observation). The banks of the Pite River are rocky (Wistrand and Lundqvist 1964) and relatively flat except in the area near Älvsbyn (Storforsen), where the difference in height between the winter low water level and the spring high water level might be over 5 m (Nilsson 1979). The Pite River crosses the former highest coastline at 220 meters above sea level (Lundqvist 1953). In northern Sweden, this coastline
was the first strip of land that was exposed between the retreating glacial ice and Ancylus Lake, a pre-stage of the Gulf of Bothnia (Cato 1985, Fromm 1985). Riparian plant communities are relatively species poor. For example, Nilsson (1979) found an average of 66 species per 200-m reach along the Pite River, which is 22 species fewer then were found in similar reaches along the Vindel River. One explanation for this may be that along the Pite River there are fewer herb species (Nilsson 1979).

Study sites were located in the riparian zones of secondary channels that had been cut off for timber floating. Fourteen sites were chosen, of which seven were channelised and seven were restored. Six of the sites were located on the Pite River itself, whereas eight sites were on tributaries to the Pite River (Tjartsebäckken and Varjisån). All but four of the sites were above the former highest coastline (Table 1A). Channelised sites were defined as secondary channels that were cut off by floatway constructions so that water levels were significantly reduced compared to the main channel. Restored sites were defined as formerly cut-off secondary channels that had been re-opened by removal of floatway constructions at least five years before the beginning of this study. Additional criteria for site selection included: 1) a relatively straight reach; 2) conditions considered to be representative for channelised and restored sites; 3) relatively stable banks, not predominantly erosive or predominantly depositional; 4) comparable slopes and substrates in the riparian zone; and 5) relatively intact riparian vegetation.

Data collection
Data were collected in August and September 2004. At each site, a 50-m long reach was randomly chosen for data collection.
Table 1A. Physical characteristics of study sites. River and riparian substrates are classified as boulder (B), cobble (C), sand (Sa) and silt (Si).

<table>
<thead>
<tr>
<th>Site number</th>
<th>River</th>
<th>Restored / Channelised</th>
<th>Former Highest coastline</th>
<th>Channel width (m)</th>
<th>River gradient (%)</th>
<th>River substrate</th>
<th>Bank gradient (%)</th>
<th>Riparian substrate</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>Pite</td>
<td>Restored Above</td>
<td>45.0</td>
<td>0.5</td>
<td>C/Sa/Si</td>
<td>2.5</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Pite</td>
<td>Restored Above</td>
<td>22.5</td>
<td>2.5</td>
<td>B/C</td>
<td>6.8</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>Pite</td>
<td>Restored Below</td>
<td>40.0</td>
<td>3.5</td>
<td>B/C/Sa</td>
<td>6.3</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>19</td>
<td>Varjisån</td>
<td>Restored Below</td>
<td>5.6</td>
<td>4.5</td>
<td>B/C</td>
<td>9.3</td>
<td>C/Sa</td>
<td></td>
</tr>
<tr>
<td>21</td>
<td>Varjisån</td>
<td>Restored Below</td>
<td>12.7</td>
<td>5.0</td>
<td>B/C</td>
<td>9.8</td>
<td>C/Sa</td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>Tjartsebäcken</td>
<td>Restored Above</td>
<td>4.4</td>
<td>2.3</td>
<td>B/C</td>
<td>1.8</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>23</td>
<td>Tjartsebäcken</td>
<td>Restored Above</td>
<td>1.7</td>
<td>1.8</td>
<td>C/Sa</td>
<td>2.3</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Pite</td>
<td>Channelised Above</td>
<td>25.0</td>
<td>1.5</td>
<td>B/C</td>
<td>9.3</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Varjisån</td>
<td>Channelised Above</td>
<td>9.0</td>
<td>2.0</td>
<td>B/C</td>
<td>1.3</td>
<td>B</td>
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<tr>
<td>9</td>
<td>Pite</td>
<td>Channelised Above</td>
<td>17.5</td>
<td>1.0</td>
<td>B/C</td>
<td>5.5</td>
<td>B</td>
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<td>10</td>
<td>Pite</td>
<td>Channelised Above</td>
<td>27.5</td>
<td>0.5</td>
<td>B/C</td>
<td>5.8</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>Varjisån</td>
<td>Channelised Below</td>
<td>4.9</td>
<td>2.5</td>
<td>B/C/Sa</td>
<td>9.8</td>
<td>C/Sa</td>
<td></td>
</tr>
<tr>
<td>24</td>
<td>Tjartsebäcken</td>
<td>Channelised Above</td>
<td>4.0</td>
<td>1.0</td>
<td>B/C</td>
<td>2.3</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>Tjartsebäcken</td>
<td>Channelised Above</td>
<td>4.1</td>
<td>0.5</td>
<td>B/C</td>
<td>3.0</td>
<td>B</td>
<td></td>
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</table>

Table 1B. Riparian forest (overstory) composition at study sites.

<table>
<thead>
<tr>
<th>Site number</th>
<th>River</th>
<th>Restored / Channelised</th>
<th>Basal area density (m² ha⁻¹)</th>
<th>% Picea abies (by m²)</th>
<th>% Pinus sylvestris (by m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>Pite</td>
<td>Restored</td>
<td>86.5</td>
<td>24</td>
<td>51</td>
</tr>
<tr>
<td>5</td>
<td>Pite</td>
<td>Restored</td>
<td>60.3</td>
<td>25</td>
<td>60</td>
</tr>
<tr>
<td>7</td>
<td>Pite</td>
<td>Restored</td>
<td>75.6</td>
<td>72</td>
<td>12</td>
</tr>
<tr>
<td>19</td>
<td>Varjisån</td>
<td>Restored</td>
<td>36.2</td>
<td>51</td>
<td>12</td>
</tr>
<tr>
<td>21</td>
<td>Varjisån</td>
<td>Restored</td>
<td>30.5</td>
<td>23</td>
<td>58</td>
</tr>
<tr>
<td>22</td>
<td>Tjartsebäcken</td>
<td>Restored</td>
<td>62.8</td>
<td>75</td>
<td>19</td>
</tr>
<tr>
<td>23</td>
<td>Tjartsebäcken</td>
<td>Restored</td>
<td>59.2</td>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>Pite</td>
<td>Channelised</td>
<td>54.9</td>
<td>67</td>
<td>9</td>
</tr>
<tr>
<td>6</td>
<td>Varjisån</td>
<td>Channelised</td>
<td>48.4</td>
<td>22</td>
<td>63</td>
</tr>
<tr>
<td>9</td>
<td>Pite</td>
<td>Channelised</td>
<td>159.3</td>
<td>0</td>
<td>25</td>
</tr>
<tr>
<td>10</td>
<td>Pite</td>
<td>Channelised</td>
<td>18.1</td>
<td>60</td>
<td>34</td>
</tr>
<tr>
<td>14</td>
<td>Varjisån</td>
<td>Channelised</td>
<td>121.8</td>
<td>30</td>
<td>29</td>
</tr>
<tr>
<td>24</td>
<td>Tjartsebäcken</td>
<td>Channelised</td>
<td>151.5</td>
<td>0</td>
<td>67</td>
</tr>
<tr>
<td>25</td>
<td>Tjartsebäcken</td>
<td>Channelised</td>
<td>36.1</td>
<td>97</td>
<td>0</td>
</tr>
</tbody>
</table>

Collection. Four transects were spaced evenly along each 50-m reach, originating at the bankfull water level and extending laterally into the riparian zone for 15 m. Along each transect the slope was measured using a hand-held clinometer, and differences in substrate texture were noted.

Along each transect, understory vegetation data were collected at six 1 m x 1 m quadrats. Quadrats were located at 0-1 m, 1-2 m, 2-3 m, 4-5 m, 9-10 m and 14-15 m from the bankfull edge. In each quadrat, the species and percent cover of all vascular plants were noted. Plant identification and nomenclature were according to Mossberg et al. (1992).

Overstory vegetation data were collected within an area of 15 m x 5 m encompassing each transect. Diameter at breast height (DBH), species and distance from bankfull water level were recorded for each tree larger than 10 cm DBH.
Physical and ecological data for each site are summarised in Tables 1A and 1B.

Data analysis
In order to evaluate species composition at channelised and restored sites, I calculated species richness and dominance of understory plants at the plot (i.e., quadrat) and site scales. At the plot scale, species richness was calculated as the total number of species encountered within each quadrat, and dominance was calculated as the percent cover of the most abundant species within each quadrat divided by the total plant cover within that quadrat. Total plant cover was calculated by summing all of the cover percentages recorded for all species within each quadrat. At the site scale, species richness was calculated as the total number of species encountered within all quadrats at each site. Site-scale dominance was calculated as the percent cover of the most abundant species at each site divided by the total plant cover at that site. The most abundant species at each site was determined according to the sum of percent cover values observed for each species in all quadrats at that site. Total plant cover at each site was calculated as the sum of percent cover values for all species divided by the total number of quadrat observed at that site.

Site-scale data were not normally distributed, necessitating the use of nonparametric analyses. I used Mann-Whitney U tests to compare site-scale species richness and dominance data, as well as overstory composition and transect (i.e., bank) gradients at channelised and restored sites. Differences in species richness and dominance between restored and channelised sites above and below the former highest coastline, in turbulent vs. tranquil reaches and in wide vs. narrow rivers were assessed using Kruskal-Wallis tests. Turbulent reaches were defined as reaches with river gradients over 3 %, and tranquil reaches were defined as reaches with river gradients below 3 %. Narrow rivers were rivers narrower than 15 m, and wide rivers were rivers wider than 15 m. Plot-scale data were normally distributed and satisfied the assumptions required for parametric analyses. To evaluate the effects of distance from the stream, a two-way analysis of variance (ANOVA) was conducted using species richness and dominance as dependant variables and restoration status (i.e., channelised vs. restored) and quadrat as factors. Statistical analyses were performed using SPSS 11.5 for Windows.

To compare patterns of species composition and abundance among different quadrats at restored and channelised sites, I used the Czekanowski index of similarity and principal components analysis (PCA). These analyses were conducted at the plot scale, with each plot representing the sum of species abundance values for all plots of the same distance. For example, $C_1$ is the sum of all 0-1 m plots at channelised sites, while $R_{15}$ is the sum of all 14-15 m plots at restored sites. Czekanowski index scores were calculated using the formula:

$$C = \frac{2W}{A + B}$$

where $A$ and $B$ are the sums of the abundance values for all of the species found in each of the two plots to be compared, and $W$ is the sum of the lesser abundance values for the species common to the two plots (Sørensen 1948). The PCA was calculated using Canoco 4.5 for Windows. The data were not log-transformed, species-weights and sample-weights were not specified, and no centering or standardization was done.

Results
Site characteristics
There were no significant differences between channelised and restored sites in terms of overstory composition or mean transect slope (Table 2). Similarly, there were no systematic differences in river substrate and riparian substrate composition, with channelised and restored
Table 2. Comparisons of site characteristics at channelised and restored sites. Data are mean values ± 1 standard error. Mann-Whitney U tests indicate no significant differences (α = 0.05) between channelised and restored sites.

<table>
<thead>
<tr>
<th>Site characteristic</th>
<th>Restored sites</th>
<th>Channelised sites</th>
<th>(P(U_{(2),7,7} &gt; U_{\text{obs}}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basal area density (m^2 ha^-1)</td>
<td>59 ± 8</td>
<td>84 ± 58</td>
<td>0.848</td>
</tr>
<tr>
<td>% <em>Picea abies</em> (by m^2)</td>
<td>30 ± 10</td>
<td>33 ± 10</td>
<td>0.701</td>
</tr>
<tr>
<td>% <em>Pinus sylvestris</em> (by m^2)</td>
<td>53 ± 12</td>
<td>39 ± 14</td>
<td>0.337</td>
</tr>
<tr>
<td>Mean transect slope (%)</td>
<td>5.3 ± 1.3</td>
<td>5.5 ± 1.3</td>
<td>0.798</td>
</tr>
</tbody>
</table>

Figure 2. Species richness (A) and evenness (B) of riparian plant communities at channelised and restored sites. Data are mean values ± 1 standard error.

sites both characterized primarily by boulders and cobbles overlaid with organic matter (Table 1A).

Species richness
At the site scale, species richness was not significantly higher at restored sites compared to channelised sites (\(U_{0.05(2),7,7} = 23.0, p = 0.848\); Fig.2A). No significant differences were detected between channelised and restored sites, even when sites were separated according to river width (\(\chi^2_3 = 2.210, p = 0.530\)) or turbulence (\(\chi^2_3 = 0.880, p = 0.830\)). When sites were separated according to the former highest coastline, there was still no significant difference between channelised and restored sites, although the relationship appears to be reversed below the former highest coastline. Restored sites below had significantly higher species richness than restored sites above (\(\chi^2_3 = 7.876, p = 0.049\); Fig.3).

At the plot scale, no significant differences were detected between channelised and restored sites (\(F_{1,5} = 0.197, p = 0.658\)), or among quadrats (\(F_{1,5} = 1.873, p = 0.099\)), although there was a trend of more species at 1-2 m, 2-3 m and 4-5 m in both restored and channelised sites (Fig. 4A). The interaction between restoration and distance was not statistically significant either (\(F_{1,5} = 0.688, p = 0.633\)). Restored sites had higher
Figure 3. Species richness of riparian plants at channelised and restored sites below and above the former highest coastline. Closed circles represent channelised sites. Open circles represent restored sites. Data are mean values ± 1 standard error.

species richness values at all quadrats except for 9-10 m and 14-15 m.

**Dominance**

No significant differences were detected in site-scale dominance values among study sites (U_{0.05(2),7,7} = 13.0, p = 0.142; Fig. 2B). None of the three evaluated factors (i.e., width, turbulence and the former highest coastline) showed any significant effect on patterns of dominance. At the plot scale, restored plots had significantly higher dominance values compared to channelised plots (F_{1,1} = 0.197 p = 0.001; Fig.4B). This relationship was consistent among all quadrats (i.e., no significant interaction effect for restoration and distance).

**Species composition**

The highest Czekanowski index similarity score was between the R1 and C3 plots (C = 0.631; Table 3). The lowest Czekanowski score was between the C1 and R15 plots (C = 0.223). When plots were combined, the two groups with the least in common were R>9 (i.e., the sum of R10 and R15) and C<2 (i.e., the sum of C1 and C2; C = 0.311). Overall (i.e., total) species compositions of channelised plots and restored plots were relatively similar (C = 0.610).

Principal components analysis suggests three distinct groups of riparian plant communities (Fig. 5). One group consists of the channelised plots C1 and C2, and is most strongly represented by *Molinia caerulea*. The second group consists of the restored plots R3, R5, R10 and R15 and is most strongly represented by *Vaccinium vitis-idaea*. The other plots constitute the third group, located intermediately between the first two. Eigenvalues for the first two axes are 0.748 and 0.116 (i.e., the first two axes explain 86.5% of variability). When the PCA was repeated with each plot representing the average rather than the sum of species abundance values for all plots of the same distances (e.g., where C1 is the average of all 0-1 m plots at channelised sites), the pattern was the same. Similarly, the results did not differ when the same analyses were conducted using log-transformed data.

**Discussion**

Nilsson et al. (2005) suggest that restoration will result in changes in flood frequencies, which in turn will result in increased productivity and diversity in the riparian zone. In tributaries of the Vindel River, Capon et al. (manuscript in preparation) found that restoration had a positive impact on riparian vegetation, with species richness and evenness increasing at restored sites compared to channelised sites. The fact that this study showed no significant differences in species richness between channelised and restored sites suggests that the processes described by these previous studies are not applicable to cut-off secondary channels of the Pite River.

The fact that restored sites below the former highest coastline had significantly greater species richness than did restored sites above the former highest coastline
Table 3. Czekanowski index scores for riparian plots at channelised and restored sites. Plots compared are the sums of channelised plots 0-1 and 1-2 m from the channel (C<2), channelised plots 9-10 and 14-15 m from the channel (C>9), restored plots 0-1 and 1-2 m from the channel (R<2), and restored plots 9-10 and 14-15 m from the channel (R>9), as well as all channelised plots (C total) and all restored plots (R total). Higher Czekanowski index scores indicate a greater degree of similarity in species composition.

<table>
<thead>
<tr>
<th></th>
<th>C&lt;2</th>
<th>C&gt;9</th>
<th>R&lt;2</th>
<th>R&gt;9</th>
<th>C total</th>
<th>R total</th>
</tr>
</thead>
<tbody>
<tr>
<td>C&lt;2</td>
<td>0.510</td>
<td>0.569</td>
<td>0.311</td>
<td>0.517</td>
<td>0.373</td>
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<tr>
<td>C&gt;9</td>
<td>0.510</td>
<td>0.555</td>
<td>0.569</td>
<td>0.455</td>
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<td>C total</td>
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<tr>
<td>R total</td>
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<td>0.500</td>
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Figure 4. Species richness (A) and evenness (B) by plot at channelised and restored sites. Closed circles represent channelised sites. Open circles represent restored sites. Data are mean values ± 1 standard error.

suggests that restoration might be more likely to enhance riparian species richness in secondary channels below the former highest coastline. Although no significant difference was detected between channelised and restored sites below the former highest coastline, this may be due to the fact that there were not enough sites in these categories to allow sufficient power to detect a difference. Below the former highest coastline, riparian soils tend to be finer and more easily eroded, whereas above the former highest coastline there are coarser, morainic substrates (Nilsson et al. 1991). Although all of the sites below the former highest coastline in this study were in turbulent reaches, where one would expect finer sediments to be washed away, the sediments there contained finer particles (Table 1A). Since these finer soils have a greater capacity for holding water and nutrients (Aber and Melillo 1991), it might be easier for plants to establish on newly exposed soils following restoration below the former highest coastline.

Patterns of turbulence (i.e., tranquil or turbulent reaches) along a river can have an important influence on source-sink dynamics (Pulliam 1988; Eriksson 1996).
Figure 5. Principal components analysis (PCA) of plot-scale species composition at channelised and restored sites. Each plot represents the sum of species abundance values for all plots of the same distance. Plots at channelised sites are represented by closed circles. Plots at restored sites are represented by open circles. *Vaccinium vitis-idaea* and *Molinia caerulea* were the two species most strongly correlated with the PCA axes.

Turbulent reaches are known to be more species rich and will function as sources of sediment, nutrients and plant propagules (erosion areas), while tranquil reaches, which have fewer species, will function as sinks (deposition areas; Nilsson and Holmström 1986). The areas most affected by channelisation were generally turbulent reaches (Nilsson *et al.* 2005), resulting in limited species richness throughout the entire river system. My results did not show this pattern, as there were no significant differences in species richness between turbulent and tranquil reaches. This may be due to the fact that my sites were cut-off secondary channels, where the differences between turbulent and tranquil reaches are most likely too subtle to influence source-sinks dynamics. Similarly, differences in channel width among secondary channels may be too subtle to influence the results.

Although the results did not show any clear differences in species richness between channelised and restored sites, there was a shift in species composition between the two treatments. This shift likely reflects the particular response of secondary channels to restoration. The cut-off secondary channels of the Pite River were never used for log transportation, and were therefore intact but partially de-watered during the period of channelisation, exposing bare soil that was suitable for new plant colonization. Despite the lower water levels, there might still have been fluvial disturbance affecting the riparian zone, as higher flows in the main channel could have overtopped floatway structures and led to higher flows in cut-off secondary channels. Because of the exposed soil and the small-scale fluvial
disturbance still affecting the area, riparian diversity might have been maintained or even enhanced at channelised sites. The reopening of these channels let more water into the channel even during low-flow conditions, likely drowning the habitats created by channelisation. Because the Pite River has a relatively flat riparian zone, the wetted channel became much wider, flooding a relatively large area, and thereby shifting the riparian zone upland into an area that had likely not been influenced by fluvial disturbance since before channelisation. This upland is predominantly dry to mesic managed forest of *P. sylvestris* and *P. abies* with an understory dominated by relatively few species of shrubs (e.g., *Vaccinium myrtillus* and *V. vitis-idaea*), and is comparatively species poor. This upland shift in the location of the riparian zone might therefore explain why dominance values were increased at restored sites relative to channelised sites.

The two species most strongly correlated with the PCA axes represent different extremes in their habitat preferences. *Molinia caerulea* is a grass that prefers moist habitats, such as the riparian zone closest to the water, while *V. vitis-idaea* is a dwarf shrub that prefers drier habitats, such as the upland *P. sylvestris* forest. The PCA results suggest a pattern of zonation for both channelised and restored sites, whereby *M. caerulea* has a higher relative abundance in plots closest to the channel (Fig. 5). The difference between the two treatments is that channelised plots are more evenly distributed, with the closest plots having less in common with the farthest plots. The pattern in restored plots is not as evident as in channelised plots, as plots R3, R5, R10 and R15 are all relatively similar. Overall, channelised plots are more strongly correlated with the abundance of *M. caerulea*, and restored plots are more strongly correlated with *V. vitis-idaea*. The fact that channelised plots are more strongly correlated with *M. caerulea* indicates that they have adapted to relatively moist conditions, which could be due to periodic flooding or a relatively high water table, which would be expected in former stream beds exposed by channelisation. The fact that many of the restored plots are more strongly correlated with *V. vitis-idaea* suggests a community of species adapted to dry conditions, which would be expected if they were outside the influence of fluvial disturbance during the period of channelisation, and have not adjusted to the new conditions present after restoration.

The fact that plots C1 and C2 constitute a separate group distinct from all other plots suggests that these plots occur in habitats not found at restored sites. This supports the hypothesis that these are new patches that were exposed because of the lower water levels caused by channelisation. Similarly, the fact that plots R10 and R15 constitute a distinct group suggests that these plots are in areas that do not exist at channelised sites, possibly because they are upland forest habitats that have shifted closer to the channel as a result of higher water levels after restoration. The fact that plots R1 and R2 have most in common with plots C3, C5, C10 and C15 further supports the hypothesis of an upland shift in the riparian zone following restoration. This shift suggests that at some sites the water levels might have risen 3 to 15 m along the ground.

The Czekanowski similarity index showed results that corroborate the PCA results. Channelised plots within 2 m had least in common with restored plots beyond 9 m from the channel, suggesting that these represent two distinct habitats.

In tributaries used for timber floating, channelisation led to more homogenous flow conditions and decreased flood frequencies, which resulted in decreased biodiversity in riparian plant communities (Nilsson et al. 2005, Capon et al. manuscript in preparation). In contrast, flood frequency was not necessarily
decreased in cut-off secondary channels, while lower water levels created new habitats for colonization by floodplain plants. Accordingly, the channelised sites examined in this study were likely not as species poor as expected, relative to restored sites. In tributaries used for timber floating, restoration created more variable water levels and increased the flood frequency, which increased riparian species richness. In contrast, restoration of cut-off side channels in the Pite River resulted in higher water levels, thereby drowning these new habitats and shifting the riparian zone upland. Since the Pite River is also in an area with relatively few species, the difference in species richness between channelised and restored sites might not be as evident as in more species rich areas, such as the Vindel River.

In boreal forests the vegetation is relatively species poor, but riparian areas tend to be disproportionately species rich. Restoration might therefore have important implications for regional patterns of biodiversity. My results suggest that riparian plant communities adjacent to secondary channels in the Pite River watershed may require more than five years to recover and adapt to post-restoration conditions after such a long time of channelisation. But as recent studies have shown, restoration will likely lead to an increase in species richness and evenness over time, as flows increase and flood disturbance regimes become more heterogeneous.

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