The role of adjacent vegetation on the recovery of riparian flora

Effect of upstream and upland vascular vegetation after stream restoration in a boreal catchment

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Abstract
Restoration of streams that were formerly channelized for timber-floating has become increasingly common. Generally, this restoration returns boulders from riparian zones to streams, leading to wider, more heterogeneous channels with slower flows. The primary goal is to enhance fish populations, but riparian vegetation is also expected to be favoured. However, increases in floristic diversity have not been observed and reasons for this slow response are still unknown. One possible explanation might be the lack of colonist pools. I therefore investigated how surrounding plant compositions influence riparian recovery. The vascular plant flora was identified in riparian sites and in adjacent upstream riparian and upland sites. Four reach types were included: unchannelized, channelized, restored and demonstration restored. Species richness and floristic similarities among types of sites and reaches were compared. Correlations with upland and upstream channel slopes were made and the importance of variation in seed floating ability was tested. The results show that unchannelized reaches were floristically similar to their adjacent upstream riparian and upland sites, whereas channelized reaches showed more different floras. Restoration created a somewhat more homogeneous flora among the three site types and demonstration restored reaches were most similar to upstream sites. Soil moisture conditions (i.e. wetland vs. forest) in the uplands had stronger impacts on species similarities than upland or upstream channel slopes. I conclude that adjacent sites are important for floristic recovery of riparian reaches and that demonstration restoration is most advantageous for riparian recovery. I recommend protection of upland sites from forestry to facilitate recovery.

Key words:
Channelization, demonstration restoration, species composition, species richness
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1. Introduction and Background

1.1 Ecological restoration
In the past decades the global awareness regarding the importance of ecological restoration has increased considerably (Aronson and Alexander 2013). Ecological restoration is defined as “the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed” (SER 2004). According to Palmer (2009), a more reasonable goal for ecological restoration is “to move a damaged system to an ecological state that is within acceptable limits relative to a less-disturbed system”.

Freshwater ecosystems are especially threatened by humans through influences such as pollution, channelization, damming and water extraction, and at the same time freshwater systems provide important ecosystem services (Tockner and Stanford, 2002). For example, they provide drinking water, food and habitats, act as buffer zones and serve as recreation areas (Baron et al. 2002; Giller et al. 2004), services which fulfil biological, societal and economic needs (Naiman et al. 2002).

1.2 Boreal riparian ecosystems
The riparian ecosystem is the zone at the interface between aquatic and terrestrial ecosystems and therefore represents an important ecosystem worldwide (Naiman and Décamp 1997). The riparian zone is defined as the temporarily flooded area along streams and rivers that is in the range between the lowest and highest water levels during the course of the year (Naiman and Décamp 1997). On a regional scale, riparian zones distinctly increase species diversity (Renöfält, Nilsson and Jansson 2005) because of their ability to spread diaspores far downstream (Goebel, Palik and Pregitzer 2003). However, if upstream communities are species-poor, recovery further downstream is difficult (Nilsson et al. 2010). Because of their dynamic character with water and sediment supply (Naiman and Décamp 1997), riparian zones may also harbour many vulnerable species (Burkart 2001).

In boreal and temperate areas the riparian vegetation is structured from land to water relative to increasing influences by floods and soil moisture (Johansson and Nilsson 2002; Ström et al. 2011). Additionally, the riparian vegetation also decreases in biomass productivity with increasing distance from the stream (Dwire et al. 2004; Ström et al. 2011). Typically, the strongest destructive processes for the whole riparian zones are floods and sediment deposition, causing physical disturbances. But at the same time they are also the most constructive processes, while creating new habitats and deposit nutrients (Helfield et al. 2007). In many northern Swedish streams and rivers where sediment deposition is low, the spring flood is usually the strongest disturbance event, which often occurs in combination with disturbance from floating ice (Lind and Nilsson 2015).

Plants disperse their propagules via dispersal agents such as animals, water or wind, of which hydrochory (dispersal by water) is most relevant for riparian plants, since floating propagules can disperse far downstream (Johansson, Nilsson and Nilsson 1996; Jansson et al. 2005). However, hydrochory is not responsible for the spread of plant propagules far upstream and into distant catchments; in such cases anemochory (dispersal by wind) and zoorchory (dispersal by animals) play more important roles (Gurnell et al. 2006; Nilsson et al. 2010; Wang et al. 2011). For dispersal to the surrounding habitats of riparian zones animals and vegetative dispersal are relevant (Riis and Sand-Jensen 2006; Nilsson et al. 2010). Renöfält, Nilsson and Jansson (2005) observed a relatively high similarity between the adjacent upland and riparian flora, concluding that riparian zones are also influenced laterally from adjacent uplands, beside diaspore dispersal along the stream channel. The geomorphic and hydraulic conditions are crucial factors in addition to the floating ability of a single seed type in hydrochoric dispersal (Mahoney and Rood 1998; Merritt and Wohl 2002). Indeed, more propagules disperse with a stronger flow (Merritt and Wohl 2002), but the chance for the propagules to settle is probably more relevant than the amount of propagules that spread...
(Riis 2008). The species richness in the riparian zone differs between calm and turbulent river sections (Renöfält, Nilsson and Jansson 2005). Since the propagules need objects such as boulders, trees or riparian vegetation to get stuck, channel morphology and hydraulics strongly influence the site where plants establish (Merritt and Wohl 2002; Riis and Sand-Jensen 2006). According to Andersson, Nilsson and Johansson (2000b), there is a positive relationship between the efficiency of the riparian zone to hold propagules and the richness of established riparian species. In fragmented landscapes and with proceeding climate change, plants may need to be able to disperse their propagules over longer distances to maintain their viability (Nilsson et al. 2010).

Since the riparian zone is strongly influenced by local temperature and precipitation changes (Nilsson et al. 2013), it can act as a first warning system (Johnson et al. 2006) with respect to climate change. Climate change will be largest in the boreal and arctic regions with severe warming and a shift in precipitation patterns (IPCC 2013). According to Nilsson et al. (2013), this will lead to an increased but less variable runoff and a stronger variety in ice regimes. The riparian zone is thus predicted to become narrower and to lose around 19% of its species until the end of the century (Ström, Jansson and Nilsson 2012).

1.3 Channelization and restoration

All over the world river channelization has been undertaken by humans, resulting in impairment of riparian habitats, which in turn causes a severe loss of biodiversity alongside streams (Allan and Flecker 1993). In northern Sweden, most streams and rivers have been strongly influenced by humans for more than a hundred years. From 1850 to 1980, they were used for timber-floating for which streams and rivers were channelized to facilitate transport of logs downstream to the saw mills on the coast (Törnlund and Östlund 2006). The Vindel River catchment in northern Sweden was used for timber floating until all timber was transported by trucks from 1977 on (Gardeström et al. 2013). In order to channelize the stream, boulders and large wood in stream and river beds were moved to the sides to straighten and smoothen the channel and cut off meanders (Törnlund and Östlund 2002; Gardeström et al. 2013). Bedrock outcrops and big boulders were removed using explosives (Gardeström et al. 2013).

Channelization affects the flora and fauna in and alongside a stream through a loss of habitats such as spawning ground for fish, caused by a decrease in channel complexity, a higher and more constant flow velocity and a stronger sediment erosion (Nilsson et al. 2005; Gardeström et al. 2013). Additionally, the interface between the terrestrial and aquatic systems has been largely separated with a layer of boulders, narrowing the extent of the riparian zone and its connecting function (Gardeström et al. 2013). Consequently, channelization has reduced species numbers and the productivity of the riparian zone (Nilsson et al. 2005). Channelized reaches act as semipermeable barriers for the longitudinal dispersal of water-dispersed propagules, since propagules either pass or fail to end up in appropriate habitats for establishment (Werth, Schödl and Scheidegger 2014). This is problematic for short-floating species that may sink before they have established or passed (Engström, Nilsson and Jansson 2009). However, according to Nilsson et al. (2015) many studies found a higher retention capacity at restored and natural sites, which is expected to promote long-floaters at these sites. In addition, the proportion of long-floating species has been found to increase with the number of stranded propagules along riparian reaches (Andersson, Nilsson and Johansson 2000b).

In the past decades, a steadily increasing number of streams and rivers have been restored worldwide under the assumption that increasing habitat heterogeneity will cause an increase of biodiversity (Palmer, Menninger and Bernhardt et al. 2010). Therefore, boulders and woody debris have been re-established in the streams, and channels have been rewidened to improve their physical structure (Harrison et al. 2004). However, according to Palmer, Menninger and Bernhardt (2010) many restoration projects have not yet shown the expected
increase in species diversity. No significant difference has been found between the species pool of restored sites compared to still channelized sites (Helfield et al. 2007). In restored streams, the width has increased and the water flow has become more diverse, including both faster and slower sections (Gardeström et al. 2013). Nevertheless, the observation of a clear increase in biodiversity is still lacking (Palmer, Menninger and Bernhardt 2010), a result which has also been found for the Vindel River catchment over a study period of 24 years (Nilsson et al. 2015). According to Baattrup-Pedersen et al. (2005) channelization leaves irreversible changes behind, such as mineralisation of organic matter in the riparian soil that cannot be altered by restoration efforts.

Within the Vindel River LIFE programme in northern Sweden, two different types of river restoration have been applied within the last years. One is called “best practice restoration”—further in this report called “restoration”—where available material from the riverbank, cobbles and small boulders are returned to the stream (Gardeström et al. 2013). An advanced type of restoration, the so-called “demonstration restoration”—further in this report called “demo restoration”—has been conducted at previously best-practice restored sites. Therefore, large boulders and big trees from the surrounding uplands have been added to the channel to re-establish more natural conditions (Gardeström et al. 2013). The main idea behind the restoration in the Vindel River catchment is to promote fish recovery and to increase habitat diversity as well as biodiversity (Polvi, Nilsson and Hasselquist 2014).

Stream restoration within the Vindel River catchment, especially the demo restoration, increases complexity within the stream and results in a complexity comparable to that of unchannelized streams, even though unchannelized streams vary strongly in complexity (Polvi, Nilsson and Hasselquist 2014). The complexity of channelized reaches, in contrast, is relatively similar among sites (Polvi, Nilsson and Hasselquist 2014). Thus, after restoration, the habitat heterogeneity increases while the recolonization of biota may still suffer from even stronger limitations, such as a lack of nearby species pools that could increase the biodiversity alongside and within the stream or pollutants in the catchment (Palmer, Menninger and Bernhardt 2010). Hence, unambiguous evidence of increasing species richness after restoration is still lacking (Nilsson et al. 2015).

Because channelization of streams and rivers was performed on the catchment scale, it has reduced the biodiversity in the whole catchment (Cornell and Lawton 1992). Consequently, if there are no diverse species pools remaining in the catchment, it is difficult for riparian plants to recover locally (Lake, Bond and Reich 2007). According to Kail and Hering (2009) upstream reaches up to a few kilometres in length play an important role for the ecological status of a given reach. However, Kail and Hering (2009) did not separate abiotic and biotic effects. The riparian zone is certainly affected through restoration, since removal of boulders from the bank increases the riparian area. This, however, is mostly only a side effect of restoration (Nilsson et al. 2015). According to Johansson et al. (2013), many restored river segments are still in use for forestry and logging takes place close to the streams. Sudden loss of forest cover changes light conditions, water budget, temperature and nutrient supply for the ground vegetation in the riparian zone (Göthe, Lepori and Malmqvist 2009; Mallik et al. 2011). Nilsson et al. (2015) suggested that the riparian forest should be taken into account for river restoration in order to promote a positive effect on the biodiversity in streams and along the riparian zone. Another reason for the lack of increase in riparian biodiversity is the relatively short time span since restoration (Hasselquist et al. 2015), because cold ecosystems are characterized by a slow decomposition rate and a short growing season (Palosuo et al. 2005).

1.4 Study aim and hypothesis
The aim of this study was to investigate the recolonization of riparian vegetation from surrounding vegetation after river restoration in the boreal Vindel River catchment. Therefore, the focus of interest laid on the adjacent riparian area upstream and upland of a
The study aim was implemented by inventorying the vegetation at upstream riparian sites and upland sites adjacent to 18 previously inventoried riparian study sites. Four reaches were unchannelized, four were channelized, and ten were restored (five reaches were restored between 2002 and 2005 and five reaches were demo restored in 2010).

The research question of the present study was whether the plant composition of a riparian site is related to its adjacent upstream riparian site or upland site. Specifically, the following hypotheses were tested:

H1: The flora in a given riparian site includes all species that are found in the riparian zone upstream of the site.
H2: The flora in a given riparian site includes all species that are found in the adjacent upland area.
H3: The relative contribution of upland and upstream species to the flora in a given riparian site is higher in demo restored and unchannelized reaches than in best-practice and channelized reaches and it is correlated to the slope of both the adjacent upstream stream channel and the upland area.
H4: The proportion of long-floating to short-floating species is higher in demo restored and unchannelized reaches than in best-practice restored and channelized reaches.

2. Material and Methods

2.1 Study site

The study was conducted in the Vindel River catchment in northern Sweden (Figure 1). The headwater of the Vindel River is in the Swedish mountains close to the Norwegian border and the river flows to the southeast, joining the Ume River 40 km before the river reaches the Gulf of Bothnia. The Vindel River is one of four large free-flowing rivers in northern Sweden with a length of 445 km, draining an area of 12650 km² (Jansson et al. 2000). The mean annual flow is about 200 m³/s at the confluence with the Ume River with a strong interannual variation of a 100 times higher discharge during the spring flood in comparison to the minimum discharge in late winter (Jansson et al. 2000; Ström, Jansson and Nilsson 2012). The length of the growing season varies between 125 and 145 days in the study area (SMHI 2015).

The 18 sampling sites, on tributaries of the Vindel River, were chosen based on earlier studies on riparian vegetation and geomorphic complexity (Polvi, Nilsson and Hasselquist 2014; Hasselquist et al. 2015). Four sample sites were placed along unchannelized streams and four along channelized streams. Five sites were situated at restored reaches and five at demo restored reaches (Figure 1). Two sites were located in the same area and under the same conditions as all other streams but in tributaries to the Ume River. All sites developed under the same geological conditions, since they are located above the former highest shoreline. In addition, all sites are surrounded by similar proportions of forest cover (Pilotto, pers. comm., 2015). The unchannelized streams need to be treated carefully as reference sites in comparison to channelized streams since they were either steeper or narrower than the impacted streams, which is why they had not been channelized for timber floating (Helfield et al. 2007).
The surrounding forest is used for timber production along all sites including restored sites and the riparian forest mainly consists of *Picea abies*, *Pinus sylvestris* with some *Alnus incana* and *Betula pubescens* (Ström, Jansson and Nilsson 2012; Johansson et al. 2013). Closer to the river, the shrub zone is mostly represented by *Salix* spp. and *Juniperus communis* and along the stream the graminoid zone consists mainly of *Carex* spp. (Ström, Jansson and Nilsson 2012; Hasselquist et al. 2015).

### 2.2 Sampling

The sampling took place in June and July 2015 at the 18 stream reaches. At each site, previously inventoried riparian reaches of 60 m length along a turbulent reach were used as a starting point for further inventories (Figure 2). At most of the sites the riparian study site was on the right side of the stream in the flow direction, but for practical reasons a few were on the left side of the stream bank. According to Renöfält, Nilsson and Jansson (2005), the upper boundary of the riparian zone is indicated by the lower limit of *Vaccinium myrtillus* stands which are intolerant to standing water. The end of a permanent cover of *Carex* spp. marks the lower boundary of the part of the riparian zone that is exposed during summer (Jansson et al. 2000). For practical reasons the study was located only on one bank of each stream reach.

The upstream riparian site was determined to be three times the length of the reach, meaning 180 m upstream along the same stream and including the entire width of the riparian zone (Figure 2). The upland site was located adjacent to the 60-m long riparian study site, with a width of 25 m inland from the riparian zone (Figure 2).

The flow velocity in the stream along the upstream riparian site was categorized into four groups (lake, pool, run and rapid) and the percentage of each category within the whole upstream site was noted. The categories lake, pool, run and rapid roughly have a slope of <0.01%, 0.01-1%, 1-3% and 2-5%, respectively (Polvi, pers. comm., 2015). The slope of the
upland site (lateral steepness) was measured with a clinometer. The upland wetland cover was identified within four categories (0–25%, 26–50%, 51–75% and 76–100% of wetland cover).

At the upstream riparian site, the vascular plants were identified by walking in at least two zigzag transects parallel to the stream, attempting to overview the entire riparian zone. Depending on the width of the riparian zone more transects were added whenever the mean width of the riparian zone was more than 10 m. Within the upland site, the vascular plants were identified using the same strategy along five zigzag transects parallel to the stream approximate 5 m apart (Figure 2).

At the demo restored reaches, the plant species inventory was repeated for the riparian study site, because they were restored in 2010 and the former inventory took place in 2013 (Hasselquist et al. 2015). In only 3 years after restoration the plants may not have recovered sufficiently after the disturbance so that additional colonization within the past 2 years was expected. At one site, the inventory was redone for the riparian study site as well, because the former study site has been recently restored. Therefore, the entire study site was moved further upstream. All species were identified and noted as present or absent, except for a few genera where the species were not identified separately (Calamagrostis spp., Epilobium spp., Hieracium spp., Salix spp., Sparganium spp. and Taraxacum spp.). Following Hasselquist et al. (2015) the species Carex juncella and Carex nigra were treated collectively.

For further analysis, the species were separated into two floating-time classes, distinguished as long-floating (≥2 days) and short-floating (<2 days) species according to Andersson, Nilsson and Johansson (2000b). Data of floating time were available for two thirds of the recorded species. This subset was assumed to be a fair representative of the entire flora.

Figure 2: Setup of sampling sites (upstream riparian and upland sites) adjacent to the riparian study site and the sampling strategy (zigzag lines) at each sampling site.
2.3 Statistical analysis

The statistical analysis was done using the program R (version 3.0.2, 2015). For the analysis of the first and second hypotheses about inclusion of upstream and upland vegetation within the riparian study site, differences in species richness were tested by ANOVAs and Kruskal-Wallis-Tests and differences among species compositions were analysed by non-metric multidimensional scalings (nMDSs) and analysis of similarities (ANOSIM). Differences in species richness among reach types and sites were tested by ANOVAs and model assumptions were tested with the Shapiro-Wilk Test for normality and Levene Test for homoscedasticity. If model assumptions were not fulfilled, the non-parametric rank sum Kruskal-Wallis Test was used. Furthermore, the species composition was analysed using nMDS, using the Raup-Crick dissimilarity index. The 22 groups listed in Table 1 were analysed using nMDS. For each individual nMDS, just the species present in the group were included; all absent species were excluded. The nMDSs were run for two dimensions with a maximum of 100 runs to find the lowest stress value. The final stress values were smaller than 0.2 (except one that was 0.22), therefore all nMDSs were represented in a two-dimensional plot. The dissimilarities in the nMDSs listed in Table 3 were tested for significant differences by using ANOSIMs with the Raup-Crick dissimilarity index.

The third hypothesis about higher relative contribution in demo restored and unchannelized reaches and correlations with the upstream channel and the upland slope was tested for dissimilarities using the Raup-Crick dissimilarity index. Comparisons were made among the upstream riparian sites and the riparian study sites and among the upland sites and the riparian study sites. A slope index of the upstream channel was calculated by using the summed proportions of the four categories (lake=1, pool=2, run=3 and rapid=4) divided by

<table>
<thead>
<tr>
<th>Reach types</th>
<th>Study sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unchannelized</td>
<td>All sites</td>
</tr>
<tr>
<td>Channelized</td>
<td>All sites</td>
</tr>
<tr>
<td>Restored</td>
<td>All sites</td>
</tr>
<tr>
<td>Demo restored</td>
<td>All sites</td>
</tr>
<tr>
<td>Unchannelized</td>
<td>Riparian study site, Upstream riparian site</td>
</tr>
<tr>
<td>Unchannelized</td>
<td>Riparian study site, Upland site</td>
</tr>
<tr>
<td>Unchannelized</td>
<td>Upstream riparian site, Upland site</td>
</tr>
<tr>
<td>Channelized</td>
<td>Riparian study site, Upstream riparian site</td>
</tr>
<tr>
<td>Channelized</td>
<td>Riparian study site, Upland site</td>
</tr>
<tr>
<td>Channelized</td>
<td>Upstream riparian site, Upland site</td>
</tr>
<tr>
<td>Restored</td>
<td>Riparian study site, Upstream riparian site</td>
</tr>
<tr>
<td>Restored</td>
<td>Riparian study site, Upland site</td>
</tr>
<tr>
<td>Restored</td>
<td>Upstream riparian site, Upland site</td>
</tr>
<tr>
<td>Demo restored</td>
<td>Riparian study site, Upstream riparian site</td>
</tr>
<tr>
<td>Demo restored</td>
<td>Riparian study site, Upland site</td>
</tr>
<tr>
<td>Demo restored</td>
<td>Upstream riparian site, Upland site</td>
</tr>
<tr>
<td>All reach types</td>
<td>Riparian study site, Upstream riparian site</td>
</tr>
<tr>
<td>All reach types</td>
<td>Riparian study site, Upland site</td>
</tr>
<tr>
<td>All reach types</td>
<td>Riparian study site</td>
</tr>
<tr>
<td>All reach types</td>
<td>Upstream riparian site</td>
</tr>
<tr>
<td>All reach types</td>
<td>Upland site</td>
</tr>
</tbody>
</table>
100, so that the slope index varies between one and four. Correlation coefficients (Pearson’s product-moment correlation) were calculated between the dissimilarity indices and both the upstream slope index and upland slope, respectively. An additional ANOVA was done among the reach types for the species dissimilarity between the riparian study site and the upstream riparian site. Additional ANOVAs were done among the reach types for the dissimilarity between riparian study sites and upland sites and also for the same comparison without outliers. Since model assumptions were not fulfilled, the non-parametric Kruskal-Wallis Test was used for these three comparisons.

The fourth hypothesis about higher proportions of long-floating species in demo restored and unchannelized reaches was also tested by using ANOVA. The percentage of long-floating species per riparian study site was compared among the four different reach types (unchannelized, channelized, restored and demo restored) and among the three site types (riparian study site, upstream riparian site and upland site). Also the absolute number of long floaters among reach types was tested. Whenever model assumptions were not fulfilled, the non-parametric Kruskal-Wallis Test was used.

3. Results

3.1 Species richness and composition

The comparison of all three different sites for each type of reach showed a significant difference in species richness (Table 2) and species composition (Figure 3) among the reach types. The unchannelized reaches showed no difference in species richness (Table 2) and an overlap in flora among all three site types (Figure 3a and Table 3). Differences in species richness were observed between the site types for the other three reach types (channelized, restored and demo restored), where the upland sites differ significantly ($p=0.04$, $p=0.01$ and $p<0.01$, respectively) from the riparian study sites and the upstream riparian sites (Table 2). The channelized and restored reaches showed a floristic separation among all three types of site (Figure 3b and 3c). For the channelized reaches the riparian study sites and the upland site as well as the upland site and the upstream riparian sites were significantly different ($p=0.04$ and $p=0.03$, respectively, Table 3). The restored reaches showed only a significant difference between the upland site and the upstream riparian site ($p=0.02$, Table 3). The demo restored reaches showed a significant difference in flora between the upland site and the riparian study site as well as between the riparian study site and the upstream riparian site ($p=0.01$ and $p=0.03$, respectively, Figure 3d and Table 3).

Table 2: Mean numbers of species, per reach type and site. Statistical test: ANOVA and if model assumptions were not fulfilled Kruskal-Wallis Test was used. Underlined values are significantly different. The asterisks show the significance levels (*=$p<0.05$ and **=$p<0.01$).

<table>
<thead>
<tr>
<th>Reach type</th>
<th>Riparian study site</th>
<th>Upstream riparian site</th>
<th>Upland site</th>
<th>Test statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unchannelized</td>
<td>43.25</td>
<td>46.75</td>
<td>28.50</td>
<td>$F = 4.23$</td>
</tr>
<tr>
<td>Channelized</td>
<td>52.50</td>
<td>50.25</td>
<td>33.00</td>
<td>$F = 4.91$    *</td>
</tr>
<tr>
<td>Restored</td>
<td>47.60</td>
<td>50.20</td>
<td>26.40</td>
<td>Chi² = 9.80   **</td>
</tr>
<tr>
<td>Demo restored</td>
<td>54.80</td>
<td>49.20</td>
<td>27.20</td>
<td>$F = 33.40$   **</td>
</tr>
</tbody>
</table>
Figure 3: Non-metric multidimensional scalings (nMDSs) of the flora in the riparian study sites, the upstream riparian sites and the upland sites, divided by reach types (unchannelized, channelized, restored and demo restored).
Table 3: Analysis of similarity (ANOSIM) for different types of reaches and sites with the $R$ value for the ANOSIM statistics. Riparian study site (wetland/forest) means the riparian study site where the upland site has wetland or forest. The asterisks show significant differences and the significance levels (*=p<0.05 and **=p<0.01).

<table>
<thead>
<tr>
<th>Type of reach</th>
<th>Sites</th>
<th>Test statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unchannelized</td>
<td>Riparian study site-Upstream site</td>
<td>-0.13</td>
</tr>
<tr>
<td>Unchannelized</td>
<td>Riparian study site-Upland site</td>
<td>0.10</td>
</tr>
<tr>
<td>Unchannelized</td>
<td>Upland site-Upstream site</td>
<td>0.15</td>
</tr>
<tr>
<td>Channelized</td>
<td>Riparian study site-Upstream site</td>
<td>0.13</td>
</tr>
<tr>
<td>Channelized</td>
<td>Riparian study site-Upland site</td>
<td>0.31 *</td>
</tr>
<tr>
<td>Channelized</td>
<td>Upland site-Upstream site</td>
<td>0.28 *</td>
</tr>
<tr>
<td>Restored</td>
<td>Riparian study site-Upstream site</td>
<td>0.12</td>
</tr>
<tr>
<td>Restored</td>
<td>Riparian study site-Upland site</td>
<td>0.18</td>
</tr>
<tr>
<td>Restored</td>
<td>Upland site-Upstream site</td>
<td>0.43 *</td>
</tr>
<tr>
<td>Demo restored</td>
<td>Riparian study site-Upstream site</td>
<td>0.00</td>
</tr>
<tr>
<td>Demo restored</td>
<td>Riparian study site-Upland site</td>
<td>0.46 **</td>
</tr>
<tr>
<td>Demo restored</td>
<td>Upland site-Upstream site</td>
<td>0.34 *</td>
</tr>
<tr>
<td>All types of reaches</td>
<td>Riparian study site</td>
<td>-0.01</td>
</tr>
<tr>
<td>All types of reaches</td>
<td>Upstream site</td>
<td>-0.06</td>
</tr>
<tr>
<td>All types of reaches</td>
<td>Upland site</td>
<td>0.07</td>
</tr>
<tr>
<td>All types of reaches</td>
<td>Upland site: Wetland-Wetland</td>
<td>0.95 **</td>
</tr>
<tr>
<td>All types of reaches</td>
<td>Riparian study site: Wetland-Wetland</td>
<td>0.70 **</td>
</tr>
<tr>
<td>All types of reaches</td>
<td>Riparian study site and upland site (Wetland-Forest)</td>
<td>0.92 **</td>
</tr>
<tr>
<td>All types of reaches</td>
<td>Riparian study site and upland site (Wetland-Forest)</td>
<td>0.76 **</td>
</tr>
<tr>
<td></td>
<td>Riparian study site (Forest)</td>
<td></td>
</tr>
</tbody>
</table>

The species richness was not significantly different among the reach types for the riparian study site ($F=1.19$ and $p=0.35$), the upstream riparian site ($F=0.85$ and $p=0.77$) or the upland site ($F=0.37$ and $p=0.49$). The comparisons of the flora of the riparian study site and the upstream riparian site showed an overlap (Figure 4). Moreover, the flora in the riparian study sites did not differ among reach types (Table 3); instead all reach types more or less overlapped in flora. The same applies for the riparian upstream reach (Table 3) and for the comparison of their flora separated by reach type (Figures 3 and 4). However, a complete inclusion of all upstream riparian species within the riparian study site was not observed.
Figure 4: Non-metric multidimensional scaling (nMDS) of the flora in the riparian study sites and the upstream riparian sites, respectively.

Figure 5: Non-metric multidimensional scaling (nMDS) of the flora in the riparian study sites and the upland sites, respectively. The two upland sites and their riparian study site marked with the asterisk (*) had more than 25% wetland in the upland site.
The flora of the riparian study site was clearly different from that of the adjacent upland site (Figure 5). The clear separation was visible for all four reach types and the flora did not differ within the upland site among reach types (Table 3). However, the two upland sites with wetter conditions (more than 25% wetland) were relatively close together and differed significantly from the other upland sites \((p=0.01, \text{Table 3})\). Their flora also differed significantly from all riparian study sites \((p=0.01, \text{Table 3})\). Nevertheless, their species composition was similar to their respective riparian study sites. Additionally, these two riparian study sites with wetter conditions in the adjacent upland sites were significantly different from the other riparian study sites \((p<0.01, \text{Table 3})\). When grouping the four sites together (two wetter upland sites and their adjacent riparian study sites), the group was highly significantly different than the upland sites \((p<0.01)\) as well as the riparian study sites \((p<0.01, \text{Table 3 and Figure 5})\).

### 3.2 Stream channel slope and upland slope

There was a significant negative correlation between the species dissimilarity between the riparian study site and the upstream riparian site and the channel slope of the upstream site (Pearson’s \(r=-0.55\) and \(p=0.02, \text{Figure 6}\)). The steeper the slope of the upstream site the more similar was the flora of the upstream riparian site and the riparian study site. However, without the two extremely high species dissimilarity values the correlation was no longer significant (Pearson’s \(r=-0.33\) and \(p=0.21\)). The comparison of species dissimilarities among reach types showed no significant differences (Chi\(^2\)=0.78 and \(p=0.85\)).

The species dissimilarity analysis between the flora in the riparian study site and the upland site did not show any significant correlation with the slope of the upland site (Pearson’s \(r=-0.23\) and \(p=0.37\)). The comparison of similarities among these two sites showed a significantly higher value for the channelized compared to the restored reach type.
Figure 7: Boxplots of the proportion of long-floating species per riparian study site for the four different reach types. The centreline represents the median, while the upper and lower ends of the box show the first and the third quantile. The whiskers represent the 10th and 90th percentiles. (Chi²=8.52 and p=0.04). However, after omission of the extremely high outlying value (0.002) no significant differences remained (Chi²=6.92 and p=0.08).

3.3 Floating ability
The comparison of the proportion of long-floaters (according to Andersson, Nilsson and Johansson (2000b)) in the riparian study sites among reach types showed no significant differences (F=0.91 and p=0.46, Figure 7), although the channelized reaches had a comparatively high median value (72%), whereas the unchannelized reach type showed the largest range of ratios (56–81%). Also the absolute number of long-floating species did not show significant differences between reach types (F=1.51 and p=0.26).

Furthermore, a significant difference (Chi²=14.25 and p<0.01) in the proportion of long-floaters could be observed between the three different sites (riparian study site, upstream riparian site and upland site). The upland site had a significantly (Chi²=14.25 and p<0.01) lower mean value (61%) compared to the riparian study site and the upstream riparian site (68% and 71%, respectively).

4. Discussion

4.1 Species richness and composition
The result that the unchannelized reaches were floristically similar across sites (riparian study site, upstream site and the upland) was in contrast to all other reach types. This emphasized the importance of applying a broader view on the vegetation surrounding a
The flora along unchannelized sites showed a fairly similar species composition at all study site types. Naiman and Dé camps (1997) stressed the importance of the interaction between the riparian zone and the upland, and Renöfält, Nilsson and Jansson (2005) found a relatively high similarity between the riparian and upland flora along the main channel of the free-flowing Vindel River. Upstream riparian sites provide important species pools for riparian sites further downstream since hydrochory is the most relevant dispersal mechanism for riparian vegetation (Gurnell et al. 2008). For the impacted reach types (channelized, restored and demo restored) the flora differed at least between two of the sites, showing that channelization has impacted the floristic richness and composition. Furthermore, it means that restoration efforts have not yet brought back the unchannelized conditions. Therefore, with respect to the flora, I suggest that unchannelized sites can act as reference sites. Species composition was fairly homogeneous on a local scale and all reaches and sites had a similar flora even though the sites varied much in upstream slope, upland slope and stream complexity (Polvi, Nilsson and Hasselquist 2014). Additionally, the nMDSs of the different reach types were only compared indirectly since separate nMDSs were compared. Helfield et al. (2012) found a stronger floristic relationship between the upland and riparian study sites in restored reaches (around 5 years after restoration) compared to still channelized sites. In the current study this was still the case even though 10-13 years had passed since restoration. The presented nMDSs showed a distinctly separate species composition between the sites of the restored reaches compared to the unchannelized reaches where the sites strongly overlapped. This could be due to the fact that a complete floristic recovery along riparian zones takes at least 25 years (Hasselquist et al. 2015). In contrast, the finding that the demo restored site gained unchannelized conditions with respect to riparian flora only 5 years after demo restoration can be viewed as a successful improvement of restoration methods. However, upland floristic influence on the riparian zone seemed to take longer. At demo restored sites the upland sites were disturbed by restoration efforts by taking large boulders and wood from uplands (Gardeström et al. 2013). The impact was still visible (Kretz, personal observation, 2015) and according to MacDonald et al. (2014) recovery after disturbance of stream upland sites takes more than 7 years depending on disturbance severity.

The fact that the reach types did not show any differences within each site type (riparian study site, upstream riparian site and upland site) neither in species richness nor in species composition could be caused by strongly distinct habitat conditions causing adapted species compositions. The influences of channelization and restoration did not distinctly change species composition among reach types on each of the three site types. The riparian sites (riparian study reach and upstream riparian site) resembled each other, probably caused by similar habitat conditions such as seasonal disturbance conditions, good water and sediment supply (Naiman and Dé camps 1997). Additionally, the upstream habitats were of special importance for local vegetation beside the factors region catchment and local site condition (Kail and Hering 2009).

A further result was that the species richness and composition in the riparian study site were similar across all reach types. This raises the question whether restoration is generally necessary for floristic reasons when channelized streams are similar to unchannelized reaches in species composition and richness. However, in the inventory a few genera were treated as one single species, which certainly leads to a loss of some species diversity. Furthermore, in this context the unchannelized reaches should be treated with some caution as reference sites. Higher values of channel slopes and larger sediment sizes were the reasons why these sites were not channelized originally (Helfield et al. 2007). This fact weakens a direct comparison among reach types within the same nMDS. Other studies support the necessity of restoration and demonstrate a difference in species composition, lower species richness, lower plant cover and more species poor functional groups for channelized compared to unimpacted streams (Andersson, Nilsson and Johansson 2000a; Jansson et al. 2000; Baattrup-Pedersen et al. 2005). The restored and demo restored study sites showed a
riparian species composition that was slightly intermediate between channelized and unchannelized reaches, as previously demonstrated by Helfield et al. (2007).

Although channelization is known to disconnect the stream from its riparian zone (Bravard et al. 1997; Leyer 2006; Gardeström et al. 2013) my data showed that the upstream vegetation was still closely related to the riparian study sites. This is in contrast to Andersson, Nilsson and Johansson (2000a), who observed a floristic lower similarity with upstream vegetation for impacted rivers. Hydrochory is highly relevant for riparian species and upstream floristic communities are important species pools for the riparian zone further downstream (Johansson, Nilsson and Nilsson 1996; Gurnell et al. 2008). Thus, the upstream flora still showed a relatively strong connection to the riparian study sites. Nevertheless, the first hypothesis about inclusion of the upstream riparian flora into the flora of the riparian study site must be rejected since the floristic species composition was similar, but not all upstream species were included in the flora of the riparian study sites. In that context it is also relevant to mention that species identification of the adjacent upstream riparian reaches took place early in summer (June/July), while at the same time the summer season 2015 started relatively late. This could have led to a lack of some late sprouting species within the riparian zone since the spring flood passed shortly before the inventory took place.

While the upland sites were mostly dry and nutrient-poor and covered by dwarf-shrub dominated coniferous forest, resulting in a species-poor plant community typical for boreal forest (Renöffält, Nilsson and Jansson 2005; Ström 2011), the floristic similarity with the riparian study site was low. Therefore, the second hypothesis about upland species inclusion in the riparian study site must be rejected as well. Besides the decrease of moisture and nutrients with increasing distance from the stream, the light availability also generally decreases (Lamb, Mallik and Mackereth 2003), caused by increasing forest cover. Shade tolerant species in the upland were not able to compete with early succession species in the riparian zone (Hart and Chen 2008), so that a different species composition developed. However, this is not the case for all reach types since unchannelized and restored reaches did show significant similarities with their upland species, which could be caused by a sufficiently long time span for species spread (Hasselquist et al. 2015).

After a disturbance such as clear-cutting of forest in the upland site, some early successional riparian species may spread into the upland since they are more resistant to overstorey harvest with increasing light availability than upland vegetation (MacDonald et al. 2014). Forestry was still going on close to the riparian zone at all reach types (Johansson et al. 2013), and this was obviously the case at one study site where a relatively recent clear-cut extended over half of the 25 m wide upland site until a distance of less than 10 m away from the stream (Kretz, personal observation, 2015). Even though the riparian zone in Sweden is protected against forestry by an unharvested buffer zone (Barklund 2009), this zone has a fixed width that does not take into account any site-specific conditions such as width of the riparian zone or groundwater fluxes (Richardson, Naiman and Bisson 2012; Kuglerová et al. 2014). Furthermore, forestry in the upland can cause erosion and influence the groundwater flow, thus distinctly changing growing conditions in the upland and the riparian zone (Kokkonen et al. 2006; Johansson et al. 2013). Clear cuts close to streams also change instream nutrient cycles (Göthe, Lepori and Malmqvist 2009), which strongly influence the instream biota (Osborne and Kovacic 1993). In contrast, other authors (Lamb, Mallik and Mackereth 2003) found that forestry in the upland does not influence the riparian zone, even if the disturbance is close to the riparian zone. To understand the leading mechanisms for species recovery and species exchange between the riparian zone and the adjacent upland site, all factors, including land use (in boreal areas mostly forestry), riparian buffer zones, groundwater flows and dispersal mechanisms such as anemochory or zoochory, need to be taken into account.
Another finding was that moisture conditions in the upland habitat were highly relevant for species composition since even 25–50% upland wetland cover changed the overall species composition of upland sites and influenced the adjacent riparian study site. Vegetation at the wetland upland sites seemed to spread and establish in adjacent riverine habitats (Ström, Jansson and Nilsson 2014) and cause a similar species composition. In the comparison of upland sites and riparian study sites, the sites influenced by a wet upland can be treated as a separate species composition group, whereas the reach type and the site appeared to be less relevant. Wetland and riparian sites have more similar moisture and light conditions compared to upland forest (Lamb, Mallik and Mackereth 2003; Ström, Jansson and Nilsson 2014), so species exchange is more likely there. Nevertheless, this result is based on a small data set since just two riparian study sites appeared to have more than 25% wetland in their upland site. Hence, further investigations with larger datasets are needed.

4.2 Stream slope and upland slope
The correlation between species dissimilarity and the upstream slope should not be overrated since even though a significant correlation appeared, there was a strong variation with a few quite deviating values. The insignificance of the correlation, when removing these two deviating values, supports this. The two outlying reaches with higher species dissimilarity both had a distinct change in channel appearance (wider and calmer) just within the next few meters upstream the riparian study site, which was the case on no other reach that distinct and close to the riparian study site (Kretz, personal observation, 2015). This shows that flow velocity, roughness and channel width distinctly determine species composition. In addition, the data showed that the five steepest upstream sites with a mean slope category ‘run’ (slope index=3) were all strongly similar in species composition. Three possible explanations are plausible for this. First, propagules from the upstream site dispersed relatively fast to the riparian study sites since high roughness velocity erodes the riparian zone and disperses propagules downstream, which can then become trapped at the riparian study sites. Secondly, the riparian study sites and the upstream riparian sites received propagules from the same species pool further upstream (Kail and Hering 2009) and a similar flora establishes at both sites. Thirdly, since all riparian study sites were located in run and rapid reaches it is also possible that upstream riparian reaches along runs and rapids provide more similar habitat conditions to establish riparian vegetation. A combination of all three explanations is most likely. In addition, it needs to be pointed out that the reaches where the slope index was 3.9 were located in the same stream. Since the riparian study sites were relatively close together, the upstream end of the riparian reach downstream (restored reach) overlapped with the riparian study site of the upstream reach (demo restored site). Hence, the flora of around 470 longitudinal meters in the riparian zone was identified and the sites showed an extremely similar species composition and slope index. It was the only stream where the demo restored site was located upstream of the restored site, and thus where the species diversity and composition of the demo restored site can influence the flora along the restored reach by propagule dispersal downstream. By using channel slope of the upstream site, the current study only provides indications for the expected floristic similarity between the adjacent riparian sites. To establish clearer relationships, further studies are needed. For example, more precise upstream slope measurements could show clearer indications of the relationships between species similarity and the longitudinal slope as hypothesised. Other studies found that the channel slope of the riparian study site (Hasselquist et al. 2015) and the ability for propagules to settle along that reach (Riis 2008) were also relevant for the composition of water dispersed species from upstream sites.

The upland slope was neither a significant determinant of species dissimilarity. The steepness varied most strongly in the unchannelized sites, but the slope did not seem to have any influence on the floristic relationship between the riparian zone and the adjacent upland. Steeper slopes probably do not change conditions for dispersal traits, such as wind or animals, which are more common in forest habitats than is hydrochory (Johansson, Nilsson and Nilsson, 1996). Thus, the slope-related hydrochoric dispersal by downhill running
surface water and occasional downhill movements of loose material seems to be of minor importance. Therefore, the hypothesis that species similarity (among riparian study sites and upland sites) correlates with the slope of the upland has to be rejected. Other slope-related aspects, such as disturbances (MacDonald et al. 2014), light availability (Lamb, Mallik, and Mackereth 2003), slope aspect (Áström et al. 2007) or groundwater influences (Kuglerova et al. 2014), could give a better understanding of the mechanisms connecting the upland flora with the riparian zone.

The hypothesised difference in species contribution between the unchannelized and demo restored to the channelized and restored reach type could not be confirmed by the current data, neither for the upstream riparian sites nor for the upland sites. However, if unchannelized and channelized sites did not differ significantly, it is unlikely that restored and demo restored sites differ since their species contribution is likely to lie in between those of channelized and unchannelized reaches. It is more likely that differences in species similarities are not as strong as expected. For the restored and demo restored reaches, the relatively short time period since restoration probably plays an important role (Hasselquist et al. 2015), which still does not explain the lack of differences between unchannelized and channelized reaches. The nMDSs show that the demo restored sites are closer to the unchannelized site and that the restored sites are in between the channelized and the unchannelized reach types, but the difference was not significant.

4.3 Floating ability
Regarding floating abilities, the fourth hypothesis regarding higher proportion of long-floaters at unchannelized and demo restored reaches has to be rejected, too. A slightly higher proportion of long-floaters in the channelized reaches was observed. This might indicate, in contrast to the expectation that restoration offers an increased chance for short-floaters to establish. Merritt, Nilsson and Jansson (2010) also did not observe a difference in floating ability for the plants occupying the margins of the regulated Ume River and the free flowing Vindel River. According to Engström, Nilsson and Jansson (2009) propagules may disperse far in channelized reaches without establishing, which could support the result that more long-floaters were found at channelized sites, since short-floaters cannot establish. The floating ability of diaspores was of minor importance along the free flowing Vindel River since high spring floods were regular enough to spread diaspores (Andersson, Nilsson and Johansson 2000b). The range of seasonal flow variations is similar for the main Vindel River and its tributaries (Gardeström et al. 2013). A regular flood along all reaches is a possible cause for the similarities in floating ability among the reach types. Nevertheless, channelized streams generally have short, but intense floods caused by higher flow velocity (Nilsson et al. 2005). Nilsson et al. (2002) observed a higher proportion of short-floaters versus long-floaters in turbulent reaches compared to tranquil reaches while all examined reaches in the present study were situated in turbulent reaches, showing that reach type seems to have a smaller impact on the long- to short-floater ratio than flow velocity.

The relatively strong variation among the unchannelized sites could have been caused by a wider range of stream complexity at these sites, which, however, had also been observed at demo restored sites (Polvi, Nilsson and Hasselquist 2014). The results of the site type comparison show that riparian zones generally host more long-floating species than non-riparian sites (upland sites). This result is in line with Johansson, Nilsson and Nilsson (1996), who found a significantly higher proportion of long-floater in river banks (70%) compared to non-riparian sites (63%). This might indicate that short-floaters are also spread by other dispersal traits to reach adjacent habitats.

4.4 Conclusion
This study shows that the flora of a riparian zone at an unchannelized stream reach shares many plant species with its adjacent upstream and upland sites. In contrast, still channelized sites were less similar to their surroundings. The earliest indications of success after
restoration seem to take place in demonstration restored reaches, which develop a flora similar to that of adjacent upstream riparian sites. In addition, plant recovery seems to be faster at places where the upstream channel is steep or similar in roughness with the riparian study site. However, further studies are needed to confirm this interaction. Regarding the adjacent upland, the moisture condition (i.e. wetland vs. forest) is more important for the floristic similarity with the riparian zone than the upland slope. Upland sites with wetland vegetation are not only different from dry upland sites with forest, they also spread their plants to the adjacent riparian zone leading to a riparian flora that differs from other riparian zones. Recovery of riparian zones adjacent to forested uplands, however, seems to be limited by a species-poor flora and multidirectional dispersal vectors. In general, more time is required to re-establish a flora that is locally as homogeneous as under unchannelized conditions. Hence, restoration efforts should be promoted soon, because climate change will cause species loss in the future. Therefore, the adjacent areas of riparian zones also need to be protected from additional impacts such as forestry.
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