Ice, wood and rocks: regulating elements in riverine ecosystems

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Abstract

Riparian ecosystems are of great importance in the landscape, connecting landscape elements longitudinally and laterally and often encompassing sharp environmental gradients in ecological processes and communities. They are influenced by fluvial disturbances such as flooding, erosion and sediment deposition, which create dynamic and spatially heterogeneous habitats that support a high diversity of species. Riverine ecosystems belong among the world's most threatened systems. In rivers throughout the world, human alterations to fluvial disturbance regimes have resulted in degraded ecosystems and species loss. For example, in Sweden, watercourses of all sizes have been channelized to facilitate timber floating, but in the last 10–20 years the impacts in some of the affected rivers have been reduced by restoration actions. The objectives of this thesis are to evaluate how riverine ecosystems in general, with specific focus on riparian communities, are affected by (1) restoration of channelized reaches by boulder replacement, (2) ice formation, and (3) restoration of in-stream wood abundance in the stream channel. Objective (1) was assessed by quantifying the retention of plant propagules in channelized and restored stream reaches and by evaluating effects on riparian plant and bryophyte communities in disconnected and re-opened side channels. Retention of plant propagule mimics was highest at low flows and in sites where boulders and large wood had been replaced into the channel. Propagules are however unlikely to establish unless they can be further dispersed during subsequent spring high flows to higher riparian elevations suitable for establishment. Thus, immigration to new suitable sites may occur stepwise. Our study demonstrates that restoration of channel complexity through replacement of boulders and wood can enhance retention of plant propagules, but also highlights the importance of understanding how restoration effects vary with flow. We detected no differences in riparian diversity between re-opened and disconnected side channels, but we did observe significant differences in species composition of both vascular plant and bryophyte communities. Disconnected sites had more floodplain species, whereas restored sites had more species characteristic of upland forest. This suggests that the reopening of side channels resulted in increased water levels, resulting in new riparian zones developing in former upland areas, but that the characteristic floodplain communities have not had time to develop in response to the restored fluvial regime. Objective (2) was approached by evaluating the effect of both natural anchor ice formation and experimentally created ice in the riparian zone. Riparian plant species richness and evenness proved to be higher in plots affected by anchor ice. Plants with their over-wintering organs above the ice sheet suffered from the treatment but the overall species richness increased in ice-treated plots. Objective (3) was evaluated by studying wood recruitment and movement, channel hydraulics, propagule retention and fish abundance in streams restored with large wood. Only one stream experienced reduced velocities after large wood addition. The large size and reduced velocity were probably also the reasons why this stream proved to be the best one in trapping natural, drifting wood. Increased retention and decreased mechanical fragmentation in large wood sites will lead to decreased loss of detritus from the site and therefore higher availability of coarse particulate organic matter which can result in more species rich shredder communities. Our study did not show that the occurrence of large wood had an important role in controlling density or biomass of brown trout.

Keywords: riparian zone, timber floating, river restoration, cut-off side channels, hydrochory, large wood, anchor ice, fish.

Introduction

Riverine ecosystems are some of the most diverse and dynamic habitats in the world. They are of great importance in the landscape. For example, riparian zones, being areas where the aquatic-terrestrial ecosystems interact (Nilsson et al. 1994, Ward et al. 1999) have the ability to regulate the flow of energy and material across the aquatic-terrestrial ecosystem boundary (Naiman and Decamps 1997), and to function as corridors for dispersal of organisms, sediment and organic matter (Naiman 2005). Riverine ecosystems have however also been centres of human activity for a long time and therefore now belong to the environments most disturbed and threatened by humans (Sala et al. 2000, Tockner and Stanford 2002). In Sweden, watercourses of all sizes have been channelized to facilitate timber floating (Törnlund 2002). Such channelization primarily affected rapids where logs could produce jams (Nilsson et al. 2005). To enhance log transport, stone piers were built to line riverbanks and cut off secondary channels and meander bends, and rivers were cleared of boulders and wood, leading to a dearth of in-stream roughness elements. These actions resulted in simplified channel morphologies, decreased flood frequencies and both spatially and temporally more homogeneous flow regimes, which limited land–water contacts, increased current velocities and sediment erosion, and reduced channel roughness (Muotka and Laasonen 2002, Muotka et al. 2002, Nilsson et al. 2005, Helfield et al. 2007). The channelization also altered the hydrologic regime leading to less frequent but more intense riparian flooding since floatway constructions shield the riparian zone from all but the most infrequent, catastrophic floods (Nilsson et al. 2005). Hence, the formation of new habitat suitable for propagule recruitment was hampered (Goodwin et al. 1997), and riparian areas became more species-poor and less productive (Helfield et al. 2007).

Riparian zones and plant dispersal

The high species richness characteristic of riparian ecosystems is a result of the hydrologic regime, i.e. the timing, duration and magnitude of flow and the rate of change in flow, which create habitats with high heterogeneity and biota which are adapted to large spatial and temporal changes (Naiman et al. 1993, Ward et al. 1999). Most riparian plant species depend on recurrent, low-intensity floods that limit competitive exclusion by dominants and create patches for colonization by opportunistic species (Boedeltje et al. 2004, Vogt et al. 2006, Gurnell et al. 2008). The ability of plants to disperse propagules by water, i.e. hydrochory, is another process of vital importance for the riparian plant communities (Nilsson et al. 2010). A river can transport several million propagules annually and deposit some of them hundreds of kilometres downstream of their sources (Nilsson and Grelsson 1990, Andersson et al. 2000, Merritt and Wohl 2006). The potential importance of hydrochory was noted early (Guppy 1891-93, Sernander 1901), but it was however not realized until the late 1980s and early 1990s that hydrochory may also structure riparian plant communities (Schneider and Sharitz 1988, Nilsson et al. 1991, Johansson et al. 1996). In recent years the ecology of plant dispersal has become an increasingly important research subject due to the potential of restored rivers to serve as dispersal corridors, aiding in ecosystem recovery (Nilsson et al. 2010), and not least because of the escalating problems associated with climate change and invasive plants (Chytry et al. 2008, Ehrenfeld 2008).

Channel morphology plays a major role in determining where plant propagules are deposited (Merritt and Wohl 2006, Riis and Sand-Jensen 2006). Most propagules are deposited along the outer curves of channel bends, on obstacles such as riparian vegetation, boulders and wood, and in areas with reduced flow velocity (Andersson et al. 2000, Engström et al. 2009). Large wood and boulders reduce current velocity, thus increasing retention and storage of water, sediment, organic matter and organisms (Lemly and Hilderbrand 2000, Faustini and Jones 2003), and deposited material can provide new surfaces for the establishment of riparian vegetation (Fetherston et al. 1995). Hydrochorous dispersal to riparian zones can accelerate rates of colonization and establishment of species and thereby create more species-rich plant communities (Jansson 2005, Gerard et al. 2008, Merritt et al. 2010).

Anchor ice

Globally, many rivers regularly experience extended periods with temperatures below 0°C, allowing ice to form and accumulate. Ice dynamics is known to set the physical template in northern streams (Prowse 2001, Rood et al. 2003), but restricted knowledge about river ice conditions makes it difficult to fully identify and quantify its ecological importance (Rood et al. 2007). In northern Sweden winter conditions constitute a significant part of the year and thereby set the parameters for many processes and functions in the ecosystem.

During winter, ice can in many cases function as an important structural component. It creates new obstacles which can override other regulating elements, such as boulders and large wood. Several factors affect the formation of different types of river ice. In small and high-gradient streams, turbulent flow prevents the formation of surface ice. Instead the open water is subjected to super-cooling with temperatures slightly below 0°C (Hirayama et al. 2002). Tiny ice crystals, frazil ice, can form and adhere to substrate particles, woody debris and macrophytes and develop anchor ice (Prowse 1994, Qu and Doering 2007). Anchor ice can accumulate in such quantities that ice dams are created (Stickler et al. 2008). Such dams may fundamentally alter flow conditions by transforming turbulent river sections into stepwise pool-rapid sections, constricting flow and in extreme cases temporarily block channels (Hirayama et al. 2002, Smith and Pearce 2002). Overbank flow due to ice dams can erode banks, deposit sediment (Ettema 2002, Smith and Pearce 2002), and foster ice formation in the riparian zone, i.e. riparian ice (Prowse 1994, 2001, Stickler et al. 2008). Riparian ice can protect the underlying vegetation from ice shoves, which otherwise would scour the banks and their vegetation (Rood et al. 2007), but can also delay and shorten the growing season for species covered in ice (Shutova et al. 2006). Plants protruding through the ice, such as evergreens, might be killed by frost drought in spring (Neuner et al. 1999). Increased pressure behind ice dams can result in breakage leading to surges of ice and water flowing downstream, which can severely impact the banks and their vegetation (Rood et al. 2003). Due to the lack of knowledge on how ice functions, winter conditions are rarely considered in river restoration (Stickler and Alfredsen 2009). Lack of knowledge also restricts the opportunities to predict how ice dynamics and related ecosystem conditions will change due to flow regulation and climate change.

River restoration

An increasing awareness of the economic, ecological and social losses due to stream degradation has promoted attempts to conserve and restore flowing waters (Palmer et al. 2004, Bernhardt et al. 2005, Dudgeon et al. 2006). Recent restoration efforts in channelized rivers in Sweden have aimed at increasing the presence of mainly in-stream boulders but also large wood, to remove structures lining the land–water boundary and to open cut-off side channels (Nilsson et al. 2005, Muotka and Syrjänen 2007). These actions resulted in reduced current velocity, more heterogeneous flow and increased channel complexity. Riparian habitats are expected to experience enhanced flood duration and deposition of organic matter and sediment, which potentially can increase primary production and plant establishment (Nilsson et al. 2005). This should in the long run favour a community composition reminiscent of pristine streams (Lepori et al. 2005, Helfield et al. 2007). These restoration actions will however also likely reduce the efficiency of downstream dispersal by hydrochory, but will probably facilitate exchange of propagules between the channel and the riparian zone.

A central aim of many restoration activities is to improve ecological structures and processes that are important for ecosystem functioning. Large wood is such a component, affecting hydraulics, channel morphology, floodplain dynamics, and ecological communities, especially in temperate and boreal regions where large wood persists for long periods of time (Keller and Swanson 1979, Fetherston et al. 1995, Gurnell et al. 2002, Kail and Hering 2005). Large wood is known to change channel morphology, forming steps and pools along small and medium-sized streams (Gippel 1995, Montgomery et al. 1995). Large wood can also reduce current velocity, thus increasing retention and storage of water, sediment, organic matter and organisms (Lemly and Hilderbrand 2000, Faustini and Jones 2003). Depositional sites provide new surfaces for the establishment of riparian vegetation (Fetherston et al. 1995). In-stream wood also provides increased habitat complexity for macroinvertebrates and fish and possibly increases food availability for stream detrivores by increasing retention of terrestrially derived organic matter (Lemly and Hilderbrand 2000).

Winter conditions will inevitably be affected by restoration efforts because protruding boulders can function as starting points for surface ice formation. In cases where turbulence is increased it may also favour the formation of anchor ice dams since protruding boulders offer more area for adhesion of frazil ice (Barrineau et al. 2005, Stickler et al. 2010). The formation of local pools and slow-flowing areas upstream of anchor ice dams will however result in closure of the water surface by ice, shortening the period of dynamic ice formation, making the net effect of restoration on ice conditions difficult to predict.

Objectives

The overall aim of this thesis is to improve the understanding of certain factors controlling the abundance and species composition of riparian and aquatic communities. Hopefully my results will provide new information that will aid in future river restoration projects. The main objectives can be summarized by the following questions:

- What effects does ice formation have on riparian vegetation along boreal forest streams?
- How does restoration of channelized rivers affect dispersal of plant propagules with water?
- What effect does the re-opening of cut-off secondary channels have on riparian plant and bryophyte communities bordering the channels?
- How does restoration with in-stream wood affect hydrological parameters such as water depth and water velocity, important ecological processes such as retentiveness, and species composition and abundance of fish in riverine ecosystems?

Study area

All study sites were situated in rapids of small and medium-sized streams in the boreal region of northern Sweden. In this part of boreal Sweden streams are characterized by tranquil reaches intersected by rapids that were channelized for timber floating but which are now being restored (Nilsson et al. 2005). Water levels are highest during spring flood in May–June and lowest during late winter. In the Vindel River's main channel, extreme spring floods are more than 100 times higher (1323 $m^3 s^{-1}$) than extreme winter low flows (9 $m^3 s^{-1}$), and 10 times higher than average flows (SMHI, The Swedish Meteorological and Hydrological Institute 1979). The discharge is lower in tributaries and smaller streams but the seasonal variation and differences between low and high flows are similar. Substrates are dominated by peat and morainic deposits (Fredén 1994). The vegetation in the area is characterized by boreal forest dominated by Scots pine *Pinus sylvestris* L. and Norway spruce *Picea abies* (L.) H. Karst. with an understorey of dwarf shrubs, bryophytes and lichens. The riparian vegetation is distinctly zoned and generally rich in herbs and graminoids, proceeding from forest communities at the top of the riverbank, to shrub communities at intermediate levels and herbaceous and graminoid communities closest to the water (Nilsson 1983, Andersson et al. 2000).

Methods

For paper I we surveyed 24 streams within a radius of 80 km from the city of Umeå in northern Sweden. In each stream we located a 150 m long study site in a run or riffle reach. In order to evaluate the regulating effect of anchor ice on riparian vegetation, the ice regime at each study site was characterized by the spatial extent of anchor and surface ice during the winter of 2005–06, using six categories of ice cover. Based on this categorisation, sites were divided into two different ice regimes; sites with frequent or abundant anchor ice formation, and sites with little or no anchor ice. In the most downstream reach at every site a study transect, consisting of four 1-m^2 large plots was placed on each side of the stream, ranging from the limit of bankfull water stage and laterally 7 m away from the channel. Along each transect, data on understorey vegetation were collected in the summers of 2006 and 2007. In addition, we watered plots during winter time to experimentally create ice in the riparian zone. For this part we selected eight of the 24 sites, of which four experienced anchor ice and four did not. In each site one study transect was placed downstream of and in close connection to one of the transects used in part 1, which also functioned as a control in this experiment. Watering was conducted during three consecutive winters (2006–09). Species composition and abundance of understorey vegetation were surveyed in the summers of 2007–09.

Papers II and IV were based on studies performed in three 2nd–3rd order tributaries to the Vindel River in the Ume River catchment. In each tributary three 60–100 m long stretches of rapids were selected: one channelized, one restored with boulders, and one restored with boulders and large wood. Treatments were defined as follows: 'channelized sites' were still affected by floatway constructions, large wood and boulders were missing from the channel but instead boulders were piled in the riparian zone; 'restored sites' were formerly channelized reaches where floatway constructions had been removed and boulders replaced (Nilsson et al. 2005); and 'boulder and large wood sites' were restored sites with wood added besides boulders, in the form of whole trees placed into the channel. In study (I) we evaluated restoration effects on hydrochory and propagule retention by quantifying the ability of sites to retain wooden cubes used as propagule mimics (Nilsson 1983, Andersson et al. 2000). We released cubes in late August–early September in 2005 during low flows and in mid May in 2006 during high flows. Approximately 5000 achenes of *Helianthus annuus* L. were also released in one tributary, coinciding with cube release, to compare dispersal patterns of achenes and wooden cubes. We also placed propagule traps, consisting of Astroturf mats, in the riparian zones along the reaches to evaluate the amount of natural propagules dispersed in the different treatments.

In paper IV, we investigated how different structural components – boulders and large wood – replaced in channels as part of the restoration action, affect the riparian and aquatic ecosystems. In particular, we sought to investigate the effects of large wood placement on (1) channel hydraulics, (2) organic matter retention and dispersal of plant propagules, (3) large wood recruitment and movement, and (4) fish abundance.

For paper III, six sites were located in cut-off secondary channels in the Pite River, and eight sites were located in cut-off secondary channels in two tributaries to the same river. Out of the fourteen sites, seven were channelized, defined as secondary channels cut-off by floatway constructions and the other seven sites were restored, defined as formerly cut-off secondary channels that had been re-opened at least five years prior to the study. At each site, a 50-m long reach consisting of four evenly spaced transects was randomly chosen for vegetation surveys. In each transect, consisting of six 1 m^2 quadrats, located from the bankfull edge and 15 m into the riparian zone, we recorded the percent cover of all bryophyte and vascular plant species <2 m in height, as well as the percent cover of bare soil, boulders, large woody debris and standing water. The slope was measured using a hand-held clinometer, and differences in substrate texture were noted. Overstorey vegetation, species and distance from bankfull water level were recorded for each tree larger than 10 cm in diameter at breast height.

Summary of papers

I. Effects of river ice on riparian vegetation

We studied both natural anchor ice formation in streams and watered plots to create experimental ice in the riparian zone. We found considerable variability, both spatially and temporally, of ice formation within sites and witnessed transformations of sites into step–pool sections, totally different from the run–riffle morphology during summer. Anchor ice formation resulted in flooding and ice formation in the riparian zone. Anchor ice also enabled these otherwise turbulent river sections to be covered by surface ice. Both natural anchor ice flooding and experimentally created ice resulted in increased riparian plant species richness, probably by acting as a disturbance agent reducing competition from dominant species and creating open patches for plant colonization. The fact that dominance was lower in anchor ice sites supports this conclusion. In contrast to natural anchor ice sites, dominance was not significantly reduced in watered plots compared to controls, indicating that our experimentally created ice cover implied sufficient disturbance to favour some species over others but not to reduce dominance. Moreover, plants at sites naturally experiencing anchor ice were less affected by the experimentally created ice. Species composition was different for plots depending on ice regime; anchor ice sites had more homogenous species composition among plots. We never observed any severe ice scours and erosion which could lead to devastating effects for the vegetation but, as hypothesized, species with overwintering organs above the ice sheet, such as dwarf shrubs, showed clear signs of damage due to ice cover. We did however not detect any difference in the species composition of evergreens, the species group most sensitive to damage of plant parts protruding through the ice, depending on ice regime. We hypothesize that (1) a delayed growing season as a result of ice might favour some species and disfavour others (Kozlov and Berlina 2002); (2) ice-covered areas might experience different nutrient fluxes, in that ground frozen for a longer time might affect the nutrient availability for plants (Jones 1999); and (3) frost-drought is detrimental for some species (Kullman and Högberg 1989, Neuner et al. 1999).

More variable weather conditions in a future, warmer climate with a predicted increase in the number of 0°C-crossings during winter and shorter duration of cold periods will trigger the formation of dynamic ice events (Beltaos et al. 2006). Channelization and flow regulation also affect the formation of ice. In regulated rivers, ice dynamics are often pronounced due to rapid changes in flow, increasing the total ice production (Stickler et al. 2010). In channelized streams without in-stream obstacles and with turbulent water, surface ice formation is delayed, keeping the water surface open and susceptible to frazil ice formation. Increasing channel heterogeneity due to in-stream restoration with boulders and wood might function as starting points for surface ice formation, reducing the susceptibility to dynamic ice events. Coarse bed particles can however also favour the formation of anchor ice dams, since it increases turbulence and offers more area for adhesion of frazil ice (Brown et al. 1994, Barrineau et al.

2005, Stickler et al. 2010). As in many other river restoration projects (Stickler et al. 2010), dynamic ice processes were not considered in the restoration. Due to the difficulty to foresee the exact timing and location of ice events, designing restoration projects remains a great challenge (Rood et al. 2007).

II. Effects of stream restoration on dispersal of plant propagules

For this article we studied the effect of increased abundance of boulders and wood on the retention of water-dispersed plant propagules. We witnessed an enhanced retention of propagule mimics in restored streams, potentially beneficial for riparian plant establishment from hydrochorous propagules. Large wood proved to be more retentive than boulders, confirming the value of large wood restoration. Boulder restoration might still be a viable alternative because in the long run it can retain naturally drifting wood, thus increasing propagule retention capacity (Søndergaard and Jeppesen 2007). We expected higher retention at high flows since this is the time when most floating propagules are dispersed and are most likely to reach riparian areas suitable for establishment. Instead, retention proved to be more efficient during low flows when mimics were effectively trapped by replaced in-stream boulders and wood. Propagules are however unlikely to germinate and seedlings establish unless they can be further dispersed to riparian zones during subsequent spring high flows (Huiskes 1995, Boedeltje et al. 2004, Wolters 2005); thus immigration to new sites may occur in a stepwise manner. We found relatively few river-dispersed propagules in the propagule traps compared to previous studies (Andersson et al. 2000, Jansson 2005, Vogt et al. 2006), and low sediment deposition, implying that propagule deposition was patchy and that the recovery of colonization sites might be slow and possibly limiting the rate of ecosystem recovery.

Our results demonstrate that restoration of channel complexity through replacement of boulders and wood is potentially important for hydrochory, but it also highlights the importance of understanding how restoration effects vary with flow. If restoration has not been designed for the flows and seasons during which important ecological processes act, the possibility for the ecosystems to recover may decrease or at worst be eliminated. One explanation for why the restored structures did not function optimally at higher flows could be that in the study area most streams are restored to function optimally during median or average flows, whereas communities often are controlled by ecological processes acting during extreme flow events.

III. Effects of river restoration on riparian biodiversity in secondary channels of the Pite River, Sweden

In this article we studied how riparian vegetation is affected by the re-opening of disconnected side channels in the Pite River catchment, northern Sweden. We found no difference in species richness between restored and disconnected side channels but we observed a shift in species composition between the two. In disconnected side channels plots closest to water were dominated by riparian species whereas these plots in restored sites typically had a species composition resembling a forested upland community. Our results are most likely showing the result of a shift in water levels due to restoration. Before restoration, floatway constructions were blocking side channels eliminating water moving through the channel, except during extreme highwater events. Riparian species were able to establish and colonize the former river channel due to the extended periods with little or no flow. Following restoration, side channels were reconnected with the main channel resulting in increased water levels, drowning species that had colonized earlier stream bed sediment. Thus the new riparian areas in restored sites constitute parts of what were upland forests during channelization. Therefore the short-term effects of restoration might be detrimental to riparian plant diversity. This situation will most likely persist until natural habitat forming processes can re-construct the floodplain environment, upland species being eliminated by floods and riparian species colonizing. A decrease in riparian biodiversity during the first years is likely, and the recovery of riparian biodiversity in disconnected side channels will probably take several more years or even decades, if recovery is limited by lack of fine-grained soils for establishment of riparian plants.

IV. Large wood restoration in boulder dominated streams

For this article we looked at the effects of restoration with large wood on riverine ecosystems. We used a soft engineering approach by adding large trees including root-wads and branches to the channels. Large wood is known to affect hydraulics, channel morphology, floodplain dynamics, and ecological communities. Stream biota are expected to experience increased habitat complexity. Reduced water velocity should increase retention of organic matter and sediment, possibly resulting in increased secondary production by offering more food to detritivores, and creating new colonization sites for plant propagules Large wood is also ecologically important since it has a key role in trapping and accumulating drifting wood in natural streams (Abbe and Montgomery 2003, Dahlström et al. 2005). To function optimally the length of such ‘key members’ (Abbe and Montgomery 1996) should preferably exceed bankfull channel width, which was the case in two out of three streams. Logs in Dergabäcken did not bridge the channel and were therefore more prone to be moved by currents. Logs were pushed towards the riparian zone and three logs drifted out from the site. Although wood was not bridging the channel and some trees were removed, Dergabäcken was the only stream experiencing reduced velocities after LW placement. The large size and reduced velocities were probably also the reasons why Dergabäcken proved to be the best stream in trapping naturally deposited, drifting wood.

Due to the increased channel heterogeneity we expected an increase in propagule retention after wood addition, but all sites retained fewer cubes in the study performed after wood addition. This mismatch was probably due to the higher discharge during the post-experiment study (Engström et al. 2009). Sites then experienced 40–300 % higher discharges than during the pre-restoration assessment. Control sites however caught considerably fewer cubes in the post-experiment study whereas the large wood sites did not. Thus, the retentiveness of control sites was reduced by the increased discharge whereas large wood sites were able to retain more cubes than the control sites during the higher discharge. This implies that restoration through placement of in-stream wood enhances retentiveness and thereby reduces losses of food resources to downstream systems (Muotka and Laasonen 2002, Lepori et al. 2005). Decreased loss of detritus from the site and therefore higher availability of coarse particulate organic matter should result in more species-rich shredder communities and a higher secondary production. There was no difference in brown trout (*Salmo trutta* L.) density or biomass before and after wood addition. We see two reasons for these findings; (1) the streams already contained sufficient amounts of physical structures providing habitat for brown trout, i.e. boulders, or (2) brown trout populations are controlled by factors operating at larger spatial larger scales.

Our results illustrate that restoration by replacement of large wood can successfully enhance some effects of boulder restoration and reverse impacts of channelization, confirming the value of large wood restoration (Kail et al. 2007, Miller et al. 2010). Replacement of wood should however be considered a temporary enhancement awaiting the riparian forest to reach a state where it by itself can support the river with wood. This illustrates the importance of managing forests around streams and rivers in a sustainable way.

Concluding remarks

Through my studies I have become increasingly aware of the devastating effects humans can have on the environment. Nature is bought and sold as if we were the only users, and although ecosystem rehabilitation is valuable and worthwhile, restoration of a few systems cannot be expected to compensate for all that has been lost. However, given that only a fraction of degraded ecosystems can be restored, it is of vital importance that restoration practices are effective. One important aim of restoration is to improve ecological structures and processes that are central for ecosystem functioning. Unfortunately, many restoration efforts are only partial, depending on poor knowledge of ecosystem functioning or competing land use interests. In addition, the ecologic success of the majority of restoration projects is not evaluated, making it hard to assess how successful restoration projects potentially can be (Bernhardt et al. 2005, Palmer et al. 2005). It is important that stream restoration work considers all attributes and processes that can influence the stream channel, including a combination of local and regional variables (Allan et al. 1997). Specifically, I stress the importance of restoring components of natural flows, because if hydrological processes are not restored properly ecological processes driven by hydrology such as propagule dispersal will be hampered, delaying or disabling recovery (II). Ecological processes that operate at large spatial scales might not respond to restoration practices usually performed at relatively small scales. For example, brown trout populations utilize different parts of streams in catchments at different time of the year, making it vital to provide all relevant components to ensure viable trout populations. Therefore stream restoration needs to adopt a landscape ecological framework to ensure proper matches between scales and targeted processes (Thompson and Lake 2010).

At present, restoration actions are targeting processes and life-stages during summer, whereas the effect on ice dynamics and its effect on both biotic and abiotic factors are unknown. In our study we show that winter and ice formation can have important implications for the riparian vegetation, with present climatic conditions and with natural flow regimes (I). Further studies should evaluate how a changing climate and flow regulation will affect ice conditions and its impact on riparian zones. Therefore, ecological evaluations of restoration activities should also include assessments of winter conditions and encompass an array of abiotic and biotic indicators since different indicators will respond to restoration at different time scales, and organisms might respond differently depending on their life-stage (Lake 2001, Lake et al. 2007).

A common assumption in ecological river restoration is that enhancing habitat complexity promotes biotic recovery and particularly biodiversity (Palmer et al. 1997, Gerhard and Reich 2000). For fish and macroinvertebrate communities, increasing habitat heterogeneity is a common restoration target. However, although widely used it has rarely been proven to be effective in river restoration projects. Instead, other stressors seem to override the positive effect of increased habitat complexity

(Stewart et al. 2009, Palmer et al. 2010). Increased biodiversity might only be achieved in streams unaffected by other stressors (Stewart et al. 2009, Miller et al. 2010). For riparian vegetation, the replacement of boulders from riparian zones to stream channels has proven to increase species richness (Helfield et al. 2007), both by providing more habitat and by modifying fluvial disturbance regimes.

Adopting multi-faceted goals in river restoration remains a major challenge since many restoration projects are driven by single-targeted directives (as in our case to restore fish populations, primarily of brown trout). Restoration programs need to prioritize and set clearly defined goals which are achievable and not compromised by other stressors operating in the catchment (Palmer et al. 2010). Many restoration projects, however, even lack a clear goal, disabling success evaluation and thereby the possibility to learn from mistakes and develop new and better restoration practices (Palmer et al. 2010).

In our case, restoration was done by replacing boulders into channelized rivers, thereby increasing habitat complexity for salmonid fish. Important ecological processes, such as hydrochory, were however also restored due to the increased channel heterogeneity. Lateral connectivity between aquatic and terrestrial ecosystems was also increased, leading to increased dispersal and retention of propagules, organic matter and sediment (II, IV), along with higher frequency and duration of floods disturbing riparian vegetation, allowing for coexistence of more plant species (Helfield et al. 2007). This will favour plant species richness and secondary production in the stream (Lepori et al. 2005, Helfield et al. 2007). Increased channel heterogeneity will however also result in decreased longitudinal connectivity, but whether or not this is associated with any negative ecological consequences is presently not known.

Even though natural flow regimes and fluvial disturbance conditions have been re-established, it might take decades for riparian plant communities to recover since other factors, such as low availability of soil, might limit recovery (III). Identifying and alleviating barriers to recovery is an important goal for studies of ecological restoration. Understanding the rate and trajectory of recovery is vital not the least given that climate change and altered human land-use patterns imply that ecosystems are rarely restored back to some historical state reminiscent of pristine conditions, but will experience novel ecological conditions.

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Sammanfattning

Strandzoner längs våra älvar och bäckar har en viktig funktion i landskapet då de fungerar som en länk mellan terrestra och akvatiska ekosystem. Den störning som vattnet bidrar till i form av översvämningar, erosion och deposition skapar mångsidiga habitat där arter med olika förutsättningar ryms, vilket leder till att strandzonen ofta har en hög mångfald av arter. Högst artrikedom återfinns i områden med en måttlig störning som återkommer med jämna mellanrum, vilket förhindrar konkurrenskraftiga arter att etablera sig. Istället gynnas arter som är sämre konkurrenter men mer störningståliga. Växters förmåga att lätt kunna sprida sina frön med vatten, så kallad hydrokori, är ytterligare en orsak till den höga artrikedomen. Strandzonen är inte bara viktig för växter, även människan har använt sig av denna miljö i århundraden, vilket har resulterat i att strandzonen också är ett av de områden som är mest påverkat av människan. På senare år har en ökad medvetenhet om vattendragens viktiga roll i ekosystemen dock bidragit till ett ökat intresse för att restaurera mänskligt störda områden.

Under perioden 1850-1970 kanaliserades vattendrag över hela norra Sverige för att kunna användas vid flottning av timmer. Bäckar och älvar rensades på stenar och död ved samtidigt som man byggde ledarmar som hindrade timret från att fastna på stranden och i sidofåror. Kanaliseringen resulterade i raka vattenfåror med höga vattenhastigheter som följd. Samtidigt förstördes den viktiga länken mellan land och vatten, och den återkommande störning som strandzonen behöver för att kunna behålla sin höga biologiska mångfald blev mer sällsynt. Under de senaste decennierna har försök till vattendragsrestaureringar gjorts genom att riva ledarmar samt återföra de stenar som togs bort under flottningen till strömfåran. Restaureringen har resulterat i mer komplexa strömfåror med lägre vattenhastighet och mer varierade vattenflöden. Kopplingen mellan land och vatten återskapades och processer som översvämning, erosion och deposition ska förhoppningsvis återigen fungera mer naturligt.

Bottenis är ett naturlig förekommande fenomen som under vintern kan förändra utseende och funktion hos ett vattendrag. Bildning av bottenis börjar när vattendragen underkyls. Då formas små iskristaller (kravis) vilka lätt fastnar i varandra och på andra objekt i vattnet. I turbulenta vattendrag rörs dessa iskristaller ner till botten där de fastnar och bildar bottenis. Bottenisen kan ansamlas i sådana mängder att isdammar bildas. Bakom dessa isdammar stiger vattennivån vilket resulterar i översvämning och isbildning i strandzonen. Följderna av isbildningarna är i dagsläget okända men de skulle kunna ha både positiva och negativa effekter på vegetationen beroende på hur allvarliga de är.

Syftet med min avhandling är huvudsakligen att utvärdera hur strandzonen påverkas av (1) timmerflottning och restaurering; hur har växters artrikedom samt fröspridning påverkats, (2) isbildning i vattendrag; hur påverkar det växters artsammansättning och mångfald, samt (3) ekologiska effekter av restaurering med iläggning av hela träd i vattendrag;

vilken effekt har träden på strandning av frön, vattenhastighet och vattendjup samt fiskpopulationer, särskilt av öring?

I den första artikeln undersökte jag hur bildningen av bottenis i bäckar påverkar strandväxter. Genom att både studera lokaler där naturlig bottenis förekommer samt att vattna vissa lokaler har vi kunnat visa att isen verkar ha en positiv effekt på växters artrikedom. Troligen fungerar isen så att arter som är känsliga för störning men duktiga på att konkurrera om plats försvinner, vilket möjliggör för arter tåliga mot isens störning att etablera sig i området. Möjligen påverkar isen även andra faktorer som exempelvis näringsprocesser, uttorkning på våren och fördröjd eller förkortad växtsäsong. Det kan vara effekten av dessa processer som vi ser men inte kan förklara i dagsläget.

I den andra artikeln undersökte jag hur kanalisering samt restaurering påverkat fröspridningen. Genom att återföra stenar och träd i vattendraget ökar chansen att frön ska kunna fastna i lokalen och etablera sig vilket i längden borde öka artrikedomen. Resultaten visade att restaureringen fungerade bättre vid låga än vid höga flöden. Vattendragssträckor restaurerade med både träd och stenar fångade flest antal frön, men eftersom de strandade vid träd och stenar under låga flöden hamnade de i svåretablerade områden. Restaureringar genomförs ofta för att fungera optimalt under medelvattenföring, men då många viktiga processer i vattendrag och strandzoner är beroende av höga flöden kan en sådan restaurering försvåra eller omöjliggöra vissa aspekter av ekosystemets återhämtning. För att få önskad effekt i framtida restaureringar bör träd och stenar vara så pass stora att de påverkar vattendraget även under höga flöden för att exempelvis frön ska kunna nå områden där de kan etablera sig

I den tredje artikeln undersökte jag hur vegetationen i vattendragets sidofåror, avstängda under timmerflottningen, har påverkats av denna isolering samt av restaureringen då sidofårorna åter öppnades. Vi kunde inte se att restaureringen ökade artrikedomen, men det fanns tydliga skillnader i artsammansättning mellan lokaler som restaurerats och de som inte restaurerats. I strandzonen kan man förvänta sig hög artrikedom i ytor nära vattnet på grund av deras störning. I de restaurerade lokalerna närmast vattnet noterade vi dock arter som vanligtvis återfinns längre in i skogen, medan vi i de avstängda sidofårorna såg mer typiska strandzonsväxter. Förklaringen till detta resultat beror troligtvis på att vattennivån höjdes avsevärt i de tidigare avstängda sidofårorna vid restaurering och delar av det som varit strandzon sedan timmerflottningen hamnade under vatten. I det tidiga stadium efter restaureringen då vi besökte områdena låg ytor med högst artrikedom under vatten medan område som tidigare legat långt från vattnet återfanns precis i vattenbrynet. Det kommer att ta tid innan strandzonen uppvisar den artsammansättning som återfanns innan kanaliseringen.

I den fjärde artikeln har jag undersökt hur restaurering med iläggning av stora träd, en vidare utveckling av återsättning av sten, påverkat strandningen av frön, och förändringar i fiskpopulationen. Resultaten visade att iläggningen av träd har en positiv inverkan på vissa studerade aspekter. En lokal hade lägre vattenhastighet efter att träd placerats i lokalen. Samma lokal fångade också mest drivved, men det fanns inga tydliga skillnader i vattendjup mellan lokalerna. Höga vattenflöden under uppföljningsstudien resulterade i att färre frön strandade, men inom uppföljningsstudien strandade mer frön i lokaler med träd än i lokaler utan träd. Strandningen av frön påverkades alltså mer negativt av det höga flödet i lokaler utan träd. Större andel organiskt material samt mindre mekanisk nedbrytning gör att organiskt material kan ackumuleras under en längre tid i vattendraget, vilket i bör leda till högre artrikedom av vattenlevande insekter efter restaurering. Detta kan leda till en ökad sekundär produktion vilket gynnar hela ekosystemet. Vi kunde inte se några positiva effekter på fiskpopulationer vilket kan bero på att stenrestaureringen lyckats skapa habitat av tillräckligt bra kvalitet. Alternativt syns effekterna på fisk först då restaureringar och undersökningar görs i större skala.

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