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Effects of stream restoration on dispersal of plant propagules

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Summary

1. Species immigration is vital for the success of restoring degraded ecosystems, but the effectiveness of enhancing dispersal following restoration is seldom evaluated. Running water is an important vector for plant dispersal. Frequency and duration of floods and channel-network complexity are important factors influencing propagule dispersal. In Sweden, these functions have been modified by channelization to facilitate timber floating, thus hampering emigration and immigration of riparian propagules.

2. During the last 10–20 years, affected watercourses have been restored by removing barriers and replacing boulders into channels. This is hypothesized to facilitate retention of water-dispersed propagules. We studied the efficiency of propagule retention following restoration by releasing propagule mimics and by placing propagule traps in the riparian zone.

3. Retention of propagule mimics was highest in sites restored with boulders and large wood. Retention occurred at both high and low flows but was most efficient during low flows when mimics were trapped by boulders and wood. Waterborne propagules ending up at such sites are unlikely to establish unless they can reach the riparian zone later. At high flows, floating propagules are more likely to reach riparian areas suitable for establishment. According to propagule traps placed at various levels of the riparian zone, deposition of plant propagules and sediments did not increase in restored sites.

4. *Synthesis and applications.* Our study not only demonstrates that restoration of channel complexity through replacement of boulders and wood can enhance retention of plant propagules, but also it highlights the importance of understanding how restoration effects vary with flow. 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. We advocate that stream restoration should be designed for optimal function during those discharges under which the ecological processes in question are most important, which in this case is, during high flow.

Key-words: channelization, discharge levels, hydrochory, propagule retention, restoration, seed dispersal, timber floating

Introduction

The ecology of plant dispersal has become an increasingly important research subject, not least because of the escalating problems associated with plant invasions into new habitats (Chytry *et al.* 2008; Ehrenfeld 2008). Rivers and their riparian zones are corridors for dispersal of plant propagules as well as inorganic and organic matter (Naiman, Décamps & McClain 2005). A river can transport several million propagules annually and deposit some of them hundreds of kilometres downstream of their sources (Nilsson & Grelsson 1990; Andersson, Nilsson & Johansson 2000; Merritt & Wohl 2006). Although the potential importance of plant dispersal by water, i.e., hydrochory was noted early (Guppy 1891–93; Sernander 1901), it was not realized until the late 1980s and early 1990s that hydrochory may also structure riparian plant communities (Schneider & Sharitz 1988; Nilsson, Gardfjell & Grelsson 1991; Johansson, Nilsson & Nilsson 1996).

Most ecological functions in streams are adjusted to their hydrologic regime, i.e. the timing, duration and magnitude of flow and the rate of change in flow (Poff *et al.* 1997). The hydrologic regime is considered to be the most important factor influencing transport and deposition of propagules along rivers (Mahoney & Rood 1998; Merritt & Wohl 2002),

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and it plays a key role in governing survival and establishment of riparian plants (Mahoney & Rood 1998; Johnson 2000; Johansson & Nilsson 2002). Many riparian 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, Rasran & Jensen 2006; Gurnell *et al.* 2008). Input of hydrochorous propagules to riparian zones may result in establishment of more species-rich plant communities (Jansson *et al.* 2005; but see Gerard *et al.* 2008). 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, implying that channel morphology plays a large part in determining where plants colonize (Merritt & Wohl 2002; Riis & Sand-Jensen 2006). Thus, rivers may be important for the migration of plant populations into new areas.

In Sweden, watercourses of all sizes have been channelized to facilitate timber floating (Törnlund & Östlund 2006). Such channelization primarily affected rapids where logs produced jams (Nilsson *et al.* 2005). Stone piers were built to line riverbanks and cut off secondary channels and meander bends, and rivers were cleared of boulders and wood. Channelization altered the structure and dynamics of the riparian ecosystem and the riparian–channel interactions, limiting land–water contacts, increasing current velocities and sediment erosion, and reducing channel roughness (Nilsson *et al.* 2005). Hence, the formation of new habitat suitable for propagule recruitment was hampered (Goodwin, Hawkins & Kershner 1997), and riparian areas became more species-poor and less productive (Nilsson *et al.* 2005). Timber floating was gradually abandoned after the 1950s as the road network was developed (Törnlund & Östlund 2002). In the last 10–20 years, some Swedish rivers affected by timber floating have been restored, primarily to improve habitat for game fish. Channel complexity has been increased by removing floatway constructions, and boulders have been added to reduce current velocity and create more heterogeneous flow. These measures are expected to enhance flood duration and favour deposition of organic matter and sediments, potentially increasing primary production and establishment of stranded plant propagules in the riparian zone (Nilsson *et al.* 2005), which should favour a community composition reminiscent of unaltered streams (Lepori *et al.* 2006; Helfield *et al.* 2007).

Large wood can determine channel morphology and form steps and pools along small and medium-sized streams (Gippel 1995; Montgomery *et al.* 1995). Large wood reduces current velocity, thus increasing retention and storage of water, sediment, organic matter and organisms (Lemly & Hilderbrand 2000; Faustini & Jones 2003). Depositional sites provide new surfaces for the establishment of riparian vegetation (Fetherston, Naiman & Bilby 1995). Although previous research has focused on the function of in-stream wood, few studies have assessed the effects of restoring in-stream wood (Reich, Kershner & Wildman 2003; Kail *et al.* 2007). Large wood resembles boulders in that it may enhance and speed up the recovery of impoverished stream ecosystems. Many boulders were blasted to facilitate log transport, leading to a dearth of in-stream roughness elements for restoration. To evaluate the importance of large in-stream wood for ecosystem recovery following restoration, we placed logs in reaches previously channelized for timber floating which had recently been restored by replacing boulders.

Despite increasing awareness of the importance of restoring natural flow regimes, few studies have examined the effects of river restoration on hydrochory, including propagule deposition, under different discharge levels (but see Wolters, Garbutt & Bakker 2005; Gurnell *et al.* 2006; Rosenthal 2006). We investigated the efficiency of propagule retention at high and low flows in restored streams formerly channelized for timber floating. We examined two types of restored stream sections and their ability to trap floating propagules by releasing propagule mimics and by placing propagule traps in the riparian zone. We hypothesized that restoration would increase the retention capacity of water-dispersed propagules, resulting in more propagules being deposited in the riparian zones, primarily during spring flood when chances for propagule transport and riparian establishment are best. The rationale behind this hypothesis is that more objects in the channel would enhance stranding by reducing current velocity and thus weaken the central jet and spread drifting propagules over a larger area. We also hypothesized that adding both boulders and large wood to streams would enhance retention compared to restoration where only boulders are replaced.

Methods

STUDY SITES

The study was conducted in three second- to third-order tributaries to Vindelälven; Dergabäcken (65°30′0″N, 15°55′2″E), Abmobäcken (65°23′2″N, 17°47′1″E) and Vällingträskbäcken (65°32′4″N, 17°8′7″E), in the Umeälven catchment. The tributaries are characterized by tranquil reaches intersected by rapids that were channelized for timber floating but are now being restored (Nilsson *et al.* 2005). During the growing season, water levels are highest in May–June and lowest in August–September. In Vindelälven'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 1979). The discharge is lower in tributaries but the seasonal variation and differences between low and high flows are similar. Spring flooding is short and intense and discharge fluctuates in response to rain (Nilsson *et al.* 1994). Substrates are dominated by peat and morainic deposits (Fredén 1994). The annual growing season (days with temperatures > 5 °C) is approximately 140 days (Ångström 1974). 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 generally rich in herbs and graminoids and is zoned, 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, Nilsson & Johansson 2000). In each tributary, three 60–100-m long sites were selected: one channelized, one restored with boulders, and one restored with boulders and large wood. Criteria for site selection included: (i) a relatively straight, high-gradient channel;

Table 1. Characteristics of the studied stream reaches. Treatments are 'Channelized' (for timber-floating), 'Restored' (with boulders) and 'Large wood' (restored with boulders and large wood). Boulder restoration (BR) was made prior to large wood replacement (LWR). The amount of wood present before LWR in 2004 is referred to as 'Background wood'. Replaced wood volume was calculated from root: shoot ratios

Stream	Catchment (km^2)	Stream order	Treatment	Altitude (m a.s.l.)	Year of BR/LWR	Background wood ($m^3 ha^{-1}$)	Replaced wood ($m^3 ha^{-1}$)
Abmobäcken	90·0	3	Channelized	330			
			Restored	340	1996		
			Large wood	330	1996/2004	55·4	242·5
Vällingträskbäcken	30·2	2	Channelized	430			
			Restored	440	1999		
			Large wood	430	1999/2004	55·4	97·9
Dergabäcken	186·6	3	Channelized	430			
			Restored	480	1995		
			Large wood	450	1995/2004	0·7	146·5

m a.s.l., metres above sea level.

(ii) conditions considered to be representative of channelized and restored states; (iii) boulder restoration occurred ≥ 6 years prior to observation; (iv) wood restoration occurred 1–2 years prior to observation; (v) riparian vegetation was not obviously affected by timber extraction or other anthropogenic influences; (vi) sites were separated by no more than 5 km of stream length; and (vii) water-levels were unaffected by dams. Treatments were defined as follows: 'channelized sites' were still affected by floatway constructions, large wood and boulders were missing from the channel, instead boulders were piled in the riparian zone; 'restored sites' were formerly channelized reaches where floatway constructions had been removed and boulders replaced ≥ 6 years earlier (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 autumn 2004, whole trees with branches and root wads were added to a 100-m long, previously restored reach at each of the streams (Table 1). Trees were uprooted and placed in the stream using a tracked forest excavator. The species used were Scots pine, Norway spruce and Downy birch *Betula pubescens* L. Since conifers tend to persist longer in streams (Harmon *et al.* 1986), pine and spruce accounted for 90% of the trees used. Trees were taken > 100 m from the bankfull channel edge to minimize effects on future large wood recruitment. Trees were placed either diagonally or perpendicular to the channel, at a minimum frequency of one per 10 m of stream length. Most trees were placed with their root wads or crowns resting in the floodplain between the summer low flow and spring high flow levels. Trees were not anchored in place to allow for restructuring and/or downstream movement following high flows.

We attempted to standardize large wood frequency among sites. The amount of wood needed to mimic pristine conditions was based on Liljaniemi *et al.* (2002) who investigated climatically similar but pristine Russian rivers where the average wood density was 332 m^3 ha^{-1} (in-stream and riparian habitats combined), and Dahlström & Nilsson (2004) who found 94 m^3 ha^{-1} of in-stream wood in a study in old-growth nature reserves in Sweden. We kept our wood addition between these values (97·9–242·5 m^3 ha^{-1}; Table 1).

PROPAGULE MIMICS

We evaluated restoration effects on propagule retention by quantifying the ability of sites to retain wooden cubes used as propagule mimics (Andersson, Nilsson & Johansson 2000). Since Andersson & Nilsson (2002) found large temporal variation in the amount of drifting propagules, with most propagules in autumn low-flows one year, and during spring high-flows the following year, we released cubes in late August–early September 2005 during low flows and in mid-May 2006 during high flows. In the low-flow situation, 1000 large (21 mm $side^{-1}$) and 1000 small (12 mm $side^{-1}$) cubes were released in each of the nine sites (three channelized, three boulder-restored and three boulder+wood-restored sites). Cubes were released approximately one river width upstream the reach and caught at the end of the reach using a fine-meshed net. In the high-flow situation, 1000 large and 950 small cubes were released 10 to 15 river widths upstream to ensure that cubes could spread across the stream despite the higher discharge. Cubes were colour-coded to site and treatment.

Before releasing cubes, the topography of each site was measured with a Geodolite 506 total station (Trimble, Sweden). The position of each stranded cube was registered with the total station 30–60 min after release, when cubes had either passed the entire reach or become trapped. Cube coordinates were entered into Surfer 8 (Golden Software, Golden, CO, USA). Approximately 5000 achenes of *Helianthus annuus* L. were released at each site in Vällingträskbäcken in 2005, coinciding with cube release, to compare dispersal patterns of achenes and wooden cubes. These achenes have distinct black and white stripes and are bigger than most native seeds, making them relatively easy to retrieve. Andersson, Nilsson & Johansson (2000) investigated the floating time of wooden cubes and *H. annuus* achenes, and after 48 days (SD = ±6·3 days), 50% of 250 cubes were still floating, whereas 50% of 1000 achenes floated after 4 days (SD = ±0·3 days). Since achenes and cubes were only left floating for a period of 1–4 h in our study, floating time should not have affected dispersal. Correlations in stranding patterns between large and small cubes and achenes were calculated (Spearman's rank correlation) by dividing each reach into consecutive 3-m segments, and summarizing numbers of cubes and achenes per segment. The channelized site had 22, the restored site 25 and the large-wood site had 27 segments. To evaluate propagule retention efficiency, we used three-way mixed effects analysis of variance (ANOVA), testing for differences between treatment and between high and low discharge. The response variable was the percentage of cubes stranded within the reach, used as a measure of retention capacity. 'Treatment' (channelized, boulder restored and boulder + large wood restored), and 'discharge' (high flows and low flows) were fixed factors whereas 'stream' (Abmobäcken, Dergabäcken and Vällingträskbäcken) was considered as random. Stranding patterns of cubes were plotted using Surfer 8. To evaluate the retention efficiency of large wood, numbers of cubes stranded against each log were counted.

NATURAL PROPAGULE DISPERSAL

Deposition of organic matter and inorganic sediments was studied over a 2-year period using traps made of Astroturf mats (Wolters *et al.* 2004). Mats were placed in the riparian zone between 21–23 September 2005 and 13–14 June 2006, and between 11–12 October 2006 and 7–8 June 2007. Thus, the study comprised both falling and rising water levels, including spring floods in late May–early June. Mats were retrieved soon after the spring floods had receded, before deposited propagules had an opportunity to germinate. In 2005, 21 mats, each 30 × 30 cm in area, were placed in each site, at three elevations; close to the continuously wetted channel (low), at an elevation judged to be flooded at least every second year (mid), and at the top of the riparian zone, where flood-sensitive species have their lowest occurrences (high). Blocks of low, mid and high mats were randomly located along the reach. In 2006, three locations were randomly chosen along the reach, and mats were placed in groups of three at each location, giving a total of 18 mats per site. Within each group, one mat was located at 'mid' and two mats at 'low' elevations. Upon retrieval of mats, we judged whether they had been inundated, and sealed them in plastic bags.

In the laboratory, mats were cleaned from matter over a table, and then rinsed with water to collect any additional matter still remaining in a 1-mm fine-meshed net. We found few vegetative propagules, such as rhizome fragments, in the deposits, and therefore, all matter was treated to maximize seed germination. All matter was dried at room temperature for 3 weeks in the 2005–2006 experiment and for 1 week in the 2006–2007 experiment before weighing. All samples from the 2005–2006 sampling were used in a germination trial to identify viable propagules. In the 2006–2007 trial, each group of mats was divided between two experiments; one of the 'low' mats was selected for analysis of inorganic and organic matter while the other mats were used in a germination trial. For this trial, we sowed retrieved matter in pots with non-sterilized planting soil in mid-July in 2006 and in late June in 2007 and kept the pots in a greenhouse to the end of November when all emerging plants had been identified to species. The thickness of matter in each pot never exceeded 1 cm. If litter amounts were deemed to affect germination, litter was removed from pots after propagules attached to it had been removed. The greenhouse relied on daylight during summer and was lit between 08·00 h and 10·00 h when days became shorter. Air temperature was always kept above 16 °C but could occasionally reach 30 °C during summer. Pots were watered regularly to keep the soil moist. Seedlings were removed after identification to prevent crowding. For the sediment deposition study, samples were dried at 60 °C for 3 days to obtain the dry mass. To determine organic content, a maximum of three samples of 1 g each from each trap were heated for 2 h in 450 °C to estimate loss-on-ignition. To compare deposition of sediment and propagules along restored and channelized reaches, we conducted a three-way ANOVA. The response variables were number of seedlings, number of species per trap, mass of mineral sediment, mass of organic matter, total matter per trap and the ratio between amounts of organic and mineral matter. Physical factors were described by three variables: 'treatment' and 'inundated' (yes or no) were considered fixed factors, whereas 'stream' was considered as random. To obtain minimal adequate models, model simplification was used to remove insignificant parameters. All analyses were performed using the R statistical package (R Development Core Team 2005).

Results

DISPERSAL AND RETENTION OF PROPAGULE MIMICS

The spatial stranding patterns of *Helianthus* achenes and wooden cubes were significantly correlated for all treatments (achenes and big cubes, and achenes and small cubes $r = 0{\cdot}66–0{\cdot}90$, $P < 0{\cdot}05$). We found it easy to retrieve stranded achenes, but did not assess the success rate. Stranding patterns for small and big cubes were significantly correlated ($r = 0{\cdot}85–0{\cdot}96$, $P < 0{\cdot}05$). More cubes were retained in boulder + wood restored than in channelized sites ($P < 0{\cdot}05$, ANOVA with Tukey's *post hoc* test, Figs 1 and 2; Supporting

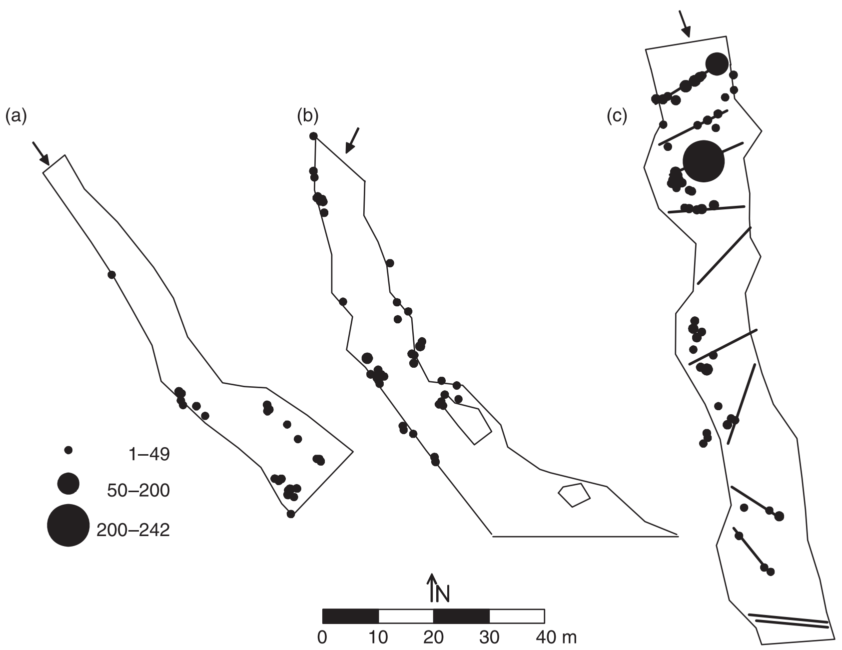

Fig. 1. Stranding patterns of small cubes in Abmobäcken; (a) channelized, (b) boulder-restored and (c) large wood + boulder restored sites. Arrows indicate flow direction, dots are stranded propagule mimics and thick lines mark the positions of logs.

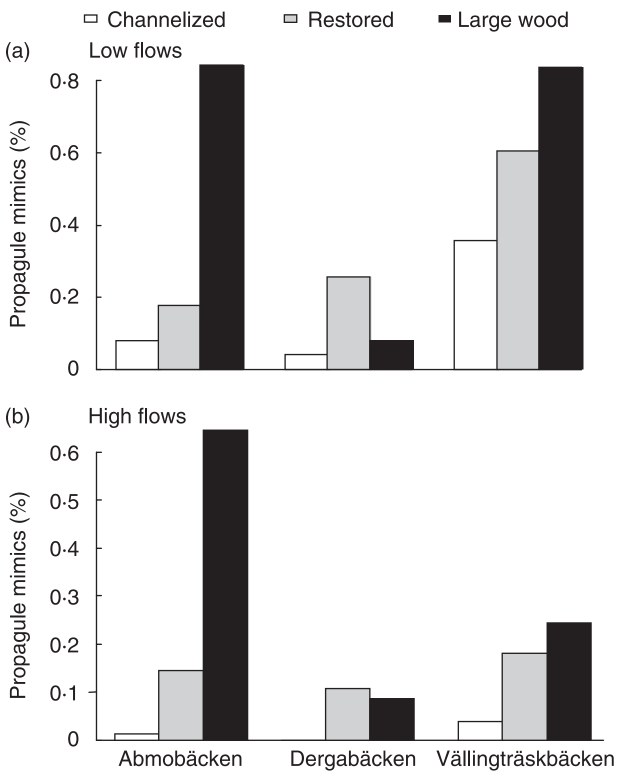

Fig. 2. Percentage of cubes trapped at (a) low discharge and (b) high discharge in the three streams at three different treatments.

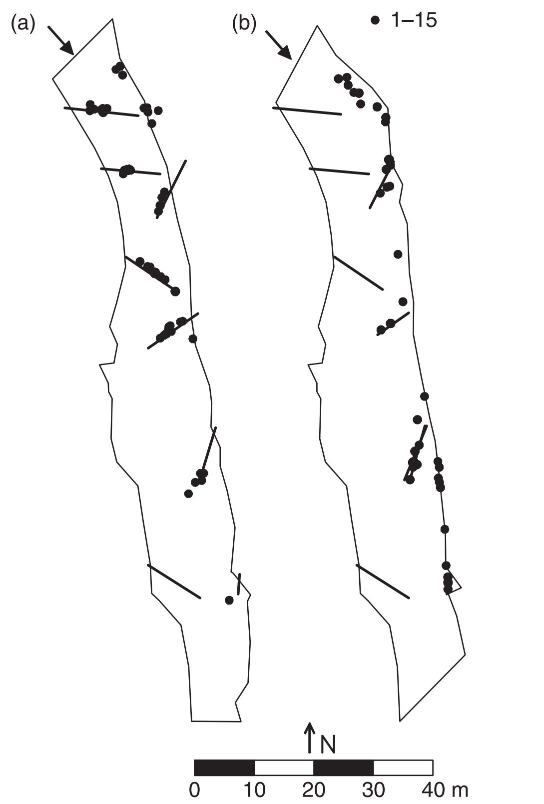

Fig. 3. Stranding pattern of propagule mimics at the large wood + boulder restored site in Dergabäcken at (a) low discharge and (b) high discharge.

Information, Table S1). The numbers of retained cubes did not differ significantly between other types of restoration, neither for small nor big cubes ($P > 0{\cdot}05$; ANOVA with Tukey's test, Fig. 2). In channelized sites, cubes were predominantly trapped at stone piers and boulder piles along the channel, preventing cubes from reaching the riparian zone (Fig. 1). In contrast, in restored sites cubes were caught by boulders and wood in or close to the riparian zone (Fig. 1). Also, more small cubes were retained during low than during high flows, but this effect was not significant for large cubes (Supporting Information, Table S1). Discharge affected not only the number of cubes trapped but also their stranding patterns. At low discharge, cubes stranded against boulders and wood in the entire site, whereas at high discharge cubes stranded in eddies, outer curves and channel expansions. At low flows, in-stream wood retained 8–29% more cubes compared to high flows (Figs 2 and 3). There was no significant difference in cube retention capacity among streams (Supporting Information, Table S1).

DEPOSITION OF PROPAGULES AND SEDIMENT

During the first-year experiment, 42 out of 189 traps were inundated during spring flood (Supporting Information, Table S3). There was no difference in the number of seedlings, number of species and total mass of deposited matter between different treatments (Supporting Information, Table S3). Neither was there any significant difference in these variables between inundated and non-inundated traps (Supporting Information, Table S3), except for a significant interaction between stream identity and treatment: the mass of deposited matter was significantly higher in Vällingträskbäcken's boulder-restored site than in Abmobäcken's channelized site ($P < 0{\cdot}05$, three-way ANOVA and Tukey test). In the second-year experiment, out of 162 traps, eight were lost and 89 were inundated during spring flood. The mean mass was $3{\cdot}0 \pm 0{\cdot}33$ g m^{-2} (mean ± SE) for non-inundated and $6{\cdot}9 \pm 1{\cdot}28$ g m^{-2} for inundated traps. The mass of deposited matter was significantly higher on inundated than on non-inundated mats (Supporting Information, Table S3). There was a significant difference between restored and channelized sites in the total mass caught. Channelized sites trapped more matter than boulder-restored sites ($P = 0{\cdot}022$, three-way ANOVA and Tukey test). This difference did not remain statistically significant when two outliers with 62·4 and 91·9 g per trap were excluded (Abmobäcken channelized site; $P = 0{\cdot}069$, Supporting Information, Table S2). No difference was found between channelized and boulder + wood sites, neither was there any difference in retention efficiency between streams (Supporting Information, Table S3). Neither mineral nor organic contents differed significantly between samples (Supporting Information, Table S4). The ratio between organic and inorganic sediment showed that channelized sites ($P < 0{\cdot}001$) and inundated mats ($P < 0{\cdot}001$, three-way ANOVAs and Tukey tests) had trapped a significantly higher proportion of inorganic than organic matter (Supporting Information, Table S4). In the germination trial (the first study year), a total of 57 seedlings of 12 species were identified (Supporting Information, Table S5); the most common species were *Solidago virgaurea* L. and *Betula pubescens* (both 18%), *Elymus caninus* L. (16%) and *Picea abies* (14%). In the germination trial (the second study year), a total of 599 seedlings of 18 species were identified (Supporting Information, Table S5); the most common species were *Betula pubescens* (72%), *Picea abies* (11%), and *Solidago virgaurea* and *Carex vaginata* Tausch. (both 2%). All species found in the germination trial are terrestrial species common in the riparian zones of the rivers studied (Supporting Information, Table S6). The number of seedlings were significantly higher on non-inundated mats ($P = 0{\cdot}034$, ANOVA); this pattern was lost when birch seeds (comprising 430 of 599 seedlings) were excluded. The number of species was close to significantly higher on non-inundated mats ($P = 0{\cdot}055$, ANOVA, Supporting Information, Table S3). The total mass of matter was not correlated with the amount of seedlings ($P = 0{\cdot}78$, $r = -0{\cdot}03$, $n = 103$), nor with the number of species ($P = 0{\cdot}51$, $r = -0{\cdot}07$, $n = 103$) that emerged during germination trials.

Discussion

Hydrochorous dispersal of plant propagules is central for the dynamics of riparian vegetation (Boedeltje *et al.* 2004; Vogt, Rasran & Jensen 2006; Gurnell *et al.* 2008), and potentially important for its recovery after restoration. Although hydrochory often results in long dispersal distances (Andersson, Nilsson & Johansson 2000), its efficiency is determined by a balance between downstream transport and functioning land–water interactions, promoting import and export of propagules to riparian zones. Floating propagules can disperse far in channelized rivers because of concentrated flow and absence of retentive structures. Recent restoration of channelized rivers has aimed to increase the presence of boulders and large wood in channels, to remove structures lining the land–water boundary, to make channels more curved, and to open cut-off channels (Nilsson *et al.* 2005; Muotka & Syrjänen 2007). These actions are likely to reduce the efficiency of downstream dispersal but will probably facilitate exchange of propagules between the channel and the riparian zone.

Despite the objective of river restoration to re-establish land–water interactions (Helfield *et al.* 2007), evaluation of ecological restoration in boreal streams generally focuses on fish (Muotka & Syrjänen 2007), overlooking other ecological processes and organisms (Nilsson *et al.* 2005). Replacement of in-stream wood is potentially important for hydrochory since wood can be a roughness element affecting flows (Gurnell *et al.* 2002). In-stream propagule dispersal increases with flow (Merritt & Wohl 2002), but available sites for colonization and establishment and not propagule numbers may be the main constraint for vegetation recovery in riparian zones (Riis 2008). In other words, propagule transport *per se* is unimportant unless propagules find proper habitats for establishment. We expected the replacement of boulders and wood to increase propagule retention during floods, but the exact nature of this process was unknown. Contrary to our hypothesis, however, fewer cubes were retained at high discharge, implying that the function of boulders and wood as retentive structures decreased during high flows when most propagules are redistributed (Supporting Information, Table S1; Figs 2 and 3), corroborating the findings of Gippel (1995) and Faustini & Jones (2003). The mismatch between propagule redistribution and trapping efficiency suggests that although more propagules are stranded at low discharge, they are likely to be trapped in boulder-dominated sites unsuitable for establishment. In contrast, propagules retained during high flows are more likely to end up in the riparian zone with appropriate conditions for establishment (Merritt & Wohl 2002). Thus, even if the retention capacity decreased at high flows, the efficiency of hydrochory, defined as numbers of retained propagules, may still be high. Depending on their floating ability and viability, propagules dispersed and trapped during autumn low flows might be further dispersed during subsequent spring high flows (Huiskes *et al.* 1995; Boedeltje *et al.* 2004; Wolters *et al.* 2005). If this is the case, restoration optimized to increase retention at low discharge could still be judged successful for riparian immigration, although immigration to new sites occurs in a stepwise manner. In concordance with Faustini & Jones (2003), large wood is more retentive than boulders, with on average more propagule mimics caught in sites with large wood added (Fig. 2; Supporting Information, Table S1). These results confirm the value of large wood restoration (Kail *et al.* 2007). Boulder restoration is still a viable alternative because in the long run large boulders may catch and retain naturally drifting wood, thus increasing propagule retention capacity (Søndergaard & Jeppesen 2007). Unimpacted turbulent reaches typically contain much large wood (Dahlström & Nilsson 2004), but in channelized reaches, wood is not easily deposited.

Dergabäcken responded differently than the other streams by trapping most cubes in the boulder-restored and not in the boulder + wood restored site (Fig. 2). This is probably because of its larger size, implying only a minor blocking effect of in-stream wood (Table 1). In Vällingträskbäcken and Abmobäcken, trees bridged the channel, whereas in Dergabäcken, trees were situated with their root wads on land and the treetops in the water. As a result, trees in Dergabäcken were more easily moved by currents, and all trees eventually pointed downstream (Fig. 3), allowing a rapid, central jet during high flows, resembling flow conditions in a channelized site (Johanna Engström, personal observations).

Flooding of riparian environments redistributes organic and inorganic matter. This provides new sites for propagule colonization (Gurnell *et al.* 2007), although thick deposits can harm propagule establishment (Xiong & Nilsson 1999). Overall, deposition of matter on our riparian traps was low, amounting to only a few grams per square metre (Supporting Information, Table S1), implying slow recovery of riparian sediment deposits in eroded channels. We hypothesized that traps in restored sites would catch more matter and propagule species, and foster more seedlings. No such trend was found; instead traps in channelized sites, during the second study year, caught more matter than traps in boulder-restored sites (Supporting Information, Table S5). Even if flooding increased the deposited mass, there was no evidence that this led to more species or seedlings, since inundated traps had fewer emerged seedlings (Supporting Information, Table S5). Traps that had escaped flooding had a disproportionately high number of birch seeds, indicating deposition of windborne seeds (Supporting Information, Table S5). Apparently, seeds deposited on traps that were later inundated were transported downstream.

The lack of difference in propagule deposition on traps between treatments seemingly contradicts results from our propagule mimic study where retention efficiency was improved by restoration. This might be an effect of high spatial aggregation of deposits, evident in the spatial pattern of cube deposition (Fig. 1). We attempted to retrieve all deposited cubes along each reach, but propagule traps were few and covered a small area, implying that deposits with many propagules were likely missed. This difference in methodology probably explains why we found relatively few river-dispersed propagules compared to previous studies in the same (Andersson, Nilsson & Johansson 2000; Jansson *et al.* 2005) and other catchments (Vogt *et al*. 2006). These authors identified and sampled concentrations of drift deposits, whereas we sampled drift deposits randomly. Other methodological issues might also have resulted in few propagules being caught and identified. Drying of collected matter might have hampered seedling emergence, since desiccation is considered to be the principal cause of propagule mortality (Merritt & Wohl 2006). This would primarily apply to non-dormant seeds that had become imbibed during water transport. A few small-seeded species not caught by tapping the mat over a table might also have slipped through the fine-meshed net during rinsing by water.

The number of propagules in riparian zones can be high (Nilsson & Grelsson 1990; Vogt *et al.* 2006), but this does not guarantee establishment. In a study by Vogt *et al.* (2006), only 1·5% of seeds found during hand-sorting emerged in a germination trial. Challenged by a seemingly high mortality of propagules, Boedeltje *et al.* (2003) tested the accuracy of their germination trial by quantifying the amount of seeds still viable after an ended experiment. They only discovered three new species and concluded that their germination results accurately represented the seeds in the samples. Thus, germination trials might be less exact than hand-sorting but can still be effective for assessing the content of viable propagules. Germination trials will however always be slightly hampered by the risk of failing to provide suitable conditions for species with specific demands (Bernhardt *et al.* 2008). We did not test the precision of our germination studies, and ended trials if no new seedlings had emerged during 1–4 weeks after the last emergence.

In conclusion, river ecologists have clearly shown that any particular site along a river is influenced by a combination of local and regional variables (Allan, Erickson & Fay 1997). Therefore, stream restoration projects need to adopt a landscape ecological framework to ensure that dispersing plant propagules can reach the specific restoration site, particularly from upstream areas. Locally, managers responsible for stream restoration need to design rivers aiming for a proper match between hydrological and targeted ecological processes. In the context of plant dispersal, a major goal should be to make flow patterns during floods more heterogeneous, thus increasing the likelihood for stranding and establishment of propagules even during high flows. Presently, most reaches are restored during low flows, and boulder replacement is not optimized for high flows. This situation could be partly remedied by placing boulders at the edge of the channel to provide turbulence and flow heterogeneity in the riparian zone during floods. Increasing retention near the centreline of the stream during floods is difficult unless available boulders and wood pieces are big enough to function even at high flows. In northern Sweden, really large trees are absent because of intensive forestry, and large boulders were blasted during channelization. Large boulders could be brought from adjacent uplands but single, large pieces of native wood are extremely rare outside reserves. Another solution would be combining large boulders and wood in piles that would function as roughness elements also during high flows. Further investigation unravelling how roughness elements affect high flows is necessary to identify best practices. However, replacement of in-stream wood should be considered a temporary action for degraded streams awaiting maturation of riparian forest and a natural recruitment process (Kail & Hering 2005; Kail *et al.* 2007).

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Supporting Information

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

Table S1. Three-way ANOVA examining differences in retention efficiency and proportion of cubes caught among channelized, boulder restored and large wood restored sites

Table S2. Mean weight per trap of total deposited mass (for both experiment years) and mean dry weight per trap of deposited sediment and organic matter (second-year experiment only)

Table S3. Three-way ANOVA, examining differences in total deposited mass among streams subjected to different treatments

Table S4. Three-way ANOVA examining differences in organic and mineral sediments trapped in different sites during the second study-year

Table S5. Number of emerged seedlings and species in each site during each year

Table S6. Species found in the germination trials

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