Recruitment of riparian plants after restoration of geomorphic complexity in northern Sweden

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Abstract

Question: Restoration of channelized streams increases geomorphic complexity but it remains unclear how this interacts with processes that drive future vegetation changes (dispersal, germination and establishment). This study asks if increased geomorphic complexity increases recruitment conditions of sown seeds or affects post-dispersal natural seedling densities.

Location: Vindel River catchment, northern Sweden.

Methods: We selected seven study streams with paired reaches that differed in the degree to which geomorphic complexity was restored. Basic reaches used simple restoration methods while enhanced reaches additionally added large boulders and woody debris. We sowed seeds of six species at ten locations in each reach in 2014 and counted the number of seedlings after 8 wk and the number of naturally occurring seedlings in a plot adjacent to the sowing locations in 2013 and 2014. Using factor analysis based on 34 complexity measurements, overall geomorphic complexity was quantified for eight of the 14 reaches.

Results: Total numbers of sown (2014) and natural seedlings (2013 and 2014) summed per reach did not differ between restoration types when tested pairwise. Enhanced restoration did not always significantly increase geomorphic complexity, which differed considerably between the streams. More complex reaches were steeper, had larger size sediment and more nutrient-poor soils. Total recruitment of sown species significantly decreased with increasing complexity. Numbers of natural seedlings differed considerably from 2013 to 2014, but were not related to complexity. In 2014, a potential parent plant of the same species occurred within the same plot for 71.8% of the natural seedlings that could be identified.

Conclusions: The recruitment of sown seeds was affected by overall geomorphic complexity rather than by the enhanced restoration. The absence of a correlation between geomorphic complexity and natural seedlings could indicate that natural seedling dynamics are not solely determined by recruitment conditions, but also by dispersal.

Introduction

Riparian zones, defined as ecosystems in the transition region between rivers and upland areas (Nilsson & Svedmark 2002), host a vegetation community that performs functions and services essential for the bordering systems. Riparian vegetation aids in resisting stream bank erosion, increasing sedimentation and controlling the input of matter and nutrients into the aquatic habitat (Naiman & Decamps 1997; Tabacchi et al. 1998). In turn, the species composition and spatial arrangement of riparian vegetation are highly regulated by the flow regime of the adjacent aquatic habitat (Nilsson & Svedmark 2002).

Many of the world's rivers and streams and their riparian zones have been degraded due to human activities such as pollution, damming, channelization and flow regulation (Dynesius & Nilsson 1994; Shafroth et al. 2002; Jansson et al. 2005; Nilsson et al. 2005). Boreal streams historically have not been strongly impacted by pollution, but instead their geomorphic complexity has been

thoroughly reduced by channelization to enable timber floating practices (Helfield et al. 2007). Geomorphic complexity is the collective term indicating the magnitude and the variability of geomorphic attributes of a reach, and is therefore determined by landscape-scale settings such as channel slope and substrate availability, as well as by the heterogeneity of these parameters (e.g. variation in sediment size) within a reach.

Since geomorphic complexity can have a large impact on the flooding regime, the simplification and homogenization of Nordic streams reduced the interaction between the river and the riparian zone, resulting in lower local plant species richness and changes in species spatial distribution (Kuglerová et al. 2016). It is therefore often assumed that increasing geomorphic complexity, e.g. by adding big boulders and more variation in sediment size, will enhance plant diversity. As expected, most restoration projects clearly demonstrate effects of restoration on geomorphic complexity (e.g. bed morphology and sediment distribution) and flow regime (Polvi et al. 2014; Nilsson et al. 2017), but effects on biota are less apparent (Hasselquist et al. 2015; Nilsson et al. 2015, 2017). In some projects, restoring geomorphic complexity from channelization increased plant or animal diversity (Helfield et al. 2007; Kuglerová et al. 2016) or shifted the spatial arrangement of species across an elevation gradient (Leyer 2005; Kuglerová et al. 2016). However, in most studies there was no change observed in riparian composition or diversity (Hasselquist et al. 2015; Nilsson et al. 2015, 2017), and nature managers therefore sometimes decide to re-restored and increased geomorphic complexity even further. However, since most studies focus primarily on reporting vegetation changes, we lack insight into the processes that may explain why or why not increased diversity is observed after increasing geomorphic complexity. We are therefore unable to address whether the enhanced restoration was necessary or if bottlenecks other than local geomorphic complexity are responsible for hampering vegetation development.

Weak and missing correlations between the species composition of deposited seeds and the standing vegetation suggest that processes like germination and establishment (together called recruitment) can have a large impact on the riparian vegetation composition and development (Lenssen et al. 1998; Andersson et al. 2000; Nilsson et al. 2010). Therefore, understanding how recruitment processes are affected by restoration of geomorphic complexity may give insight into why a change in the vegetation community does not always follow restoration.

Previous research has shown that restoration from channelization increases the survival of sunflower seeds (Dietrich et al. 2015). Recruitment of sown seeds is most likely affected by restoration due to its effect on habitat characteristics such as soil moisture and soil quality (e.g. organic matter content; Dietrich et al. 2015; Sutfin et al. 2016). On the other hand, natural recruitment may not only be affected by habitat conditions, but also by the effects of geomorphic complexity on dispersal. The main form of dispersal to riparian zones (hydrochory) is determined by the flow and flooding regime, and thus dependent on geomorphic complexity (Johansson et al. 1996; Nilsson et al. 2010). Since larger geomorphic complexity would enhance seed retention and stranding (Andersson et al. 2000; Casanova & Brock 2000; Gurnell et al. 2008; Nilsson et al. 2010), natural recruitment may be enhanced by restoring geomorphic complexity through both improved habitat conditions and better dispersal. To experimentally test the effects of geomorphic complexity and restoration on recruitment, we performed a seed addition experiment in the riparian zones of tributaries to the Vindel River in northern Sweden, and compared the recruitment of sown seeds to patterns of natural seedling recruitment. Whereas sown seeds reflect the effects of habitat conditions on recruitment without seed dispersal limitations, patterns in natural seedlings are the result of both dispersal and recruitment.

In the Vindel tributaries, geomorphic complexity was severely decreased by channelization in the 19th and 20th centuries to enable timber floating (Törnlund & Östlund 2002). From 2000 onwards, geomorphic complexity was first increased with basic restoration efforts, then increased even further in several stream reaches by more enhanced restoration activities in 2010. Recent studies show that this enhanced restoration increased geomorphic complexity and that flow velocity decreased but vegetation diversity was not affected (Kuglerová et al. 2016; Nilsson et al. 2017). One hypothesis is that such changes need more time than the few years used in these studies (Hasselquist et al. 2015; Kuglerová et al. 2016; Nilsson et al. 2017). We hypothesized that differences in recruitment could induce such future vegetation changes, and thus aimed to test the relationship between geomorphic complexity and recruitment of sown and natural seedlings. Due to the assumed positive effect of geomorphic complexity on recruitment conditions, we first hypothesized higher recruitment of sown seeds in enhanced restored reaches compared to less extensive, basic restored reaches, and similarly, we hypothesized a positive relationship between reach geomorphic complexity and recruitment. Second, we hypothesized that if we were to find a similar positive relationship between geomorphic complexity and natural seedlings as well as a correlation between numbers of sown and natural seedlings, this would indicate that dispersal is not important for natural recruitment. However, finding a different or no relationship of natural seedlings with geomorphic

complexity or with sown seedlings would indicate that dispersal alters the recruitment patterns determined by recruitment conditions alone. Third, we assumed that enhanced restoration would allow more interaction between the river and the riparian zone, and thus more hydrochorous seed dispersal (van Leeuwen et al. 2014; Hasselquist et al. 2015; Kuglerová et al. 2015), which typically transports seeds over longer distances compared to wind. We therefore expected that in enhanced reaches, long-distance dispersal would be more common compared to basic reaches and thus that potential parent plants exist nearby less frequently in enhanced reaches compared to basic reaches.

Methods

Site description

Study sites were located in seven tributaries in the Vindel River catchment in northern Sweden (Fig. 1). The free-flowing Vindel River spans 450 km from its origin to the Baltic Sea and has a mean daily discharge of 190 $m^3 \cdot s^{-1}$ (since 1980; Swedish Meteorological and Hydrological Institute). Water levels in the tributaries fluctuate rapidly due to precipitation events, and spring flooding causes predictable flooding between the middle of May to mid-June (Helfield et al. 2007). The riparian zones are generally rocky, between ca. 1- and 10-m wide, and are vegetated with mixed forest of birch (*Betula* spp.) and pine (*Pinus sylvestris*) at higher elevations, shrub communities with high abundance of European blueberry (*Vaccinium myrtillius*) somewhat closer to the stream, and diverse graminoid and forb communities at lower elevations (Nilsson et al. 1994; Helfield et al. 2007).

Restoration of geomorphic complexity

Within seven streams, we selected a pair of reaches (Fig. 1a) with different types of restoration. From 2002 to 2005, coarse sediment on the banks (the leftover material from channelization) was moved back into the stream channel (Fig. 1b), producing what is henceforth referred to as basic reaches. Subsequently, the previously executed basic restoration was enhanced in 2010 in some reaches by moving large boulders and large woody debris from upland areas into the stream channel and arranging them to substantially increase geomorphic complexity (Fig. 1c), producing what is henceforth referred to as enhanced reaches (Gardeström et al. 2013; Nilsson et al. 2017). Within each stream, basic (upstream) and enhanced (downstream) reaches are separated by at least 1 km or a lake-like section. A more detailed description of the reaches can be found in Appendix S1 (Gardeström et al. 2013; Polvi et al. 2014; Nilsson et al. 2017).
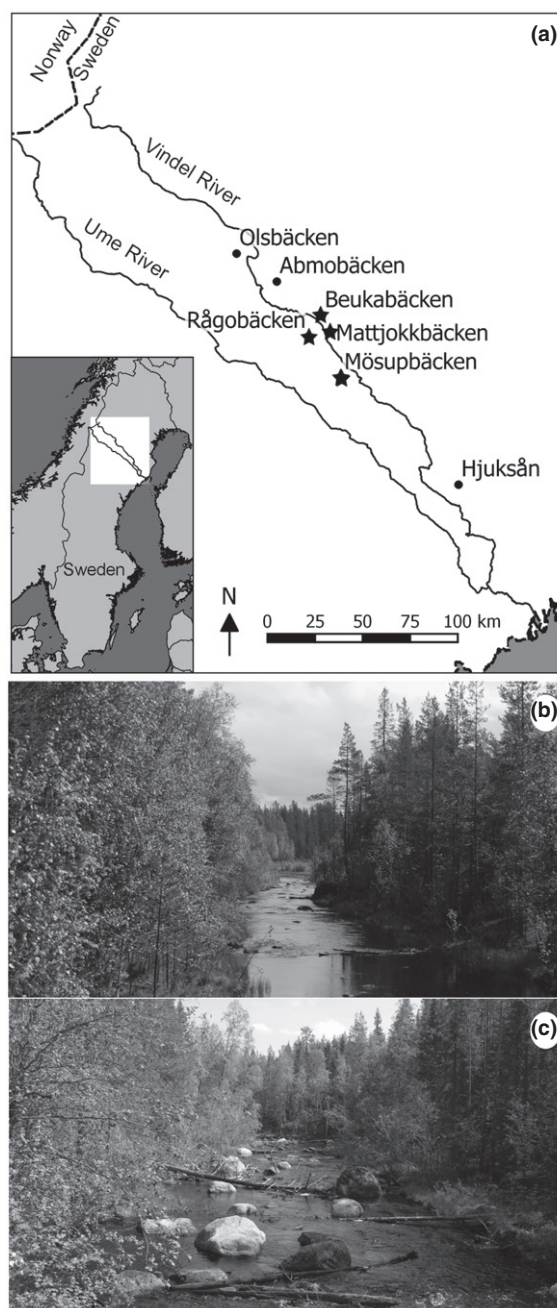
Fig. 1. (**a**) The seven study tributaries along the Vindel River in northern Sweden with pairs of basic and enhanced reaches. Streams included where detailed geomorphic complexity measures were measured (Polvi et al. 2014) are indicated with an asterisk. Created with QGIS. (**b**) Stream reaches restored with the basic, best practice technique and (**c**) the enhanced technique in the Mösupbäcken tributary. Photos: Erik Herberg.

Experimental setup

We selected ten locations along 100 m of one bank, distributed across the riparian zone at different elevations according to the template in Fig. 2. At each location, we
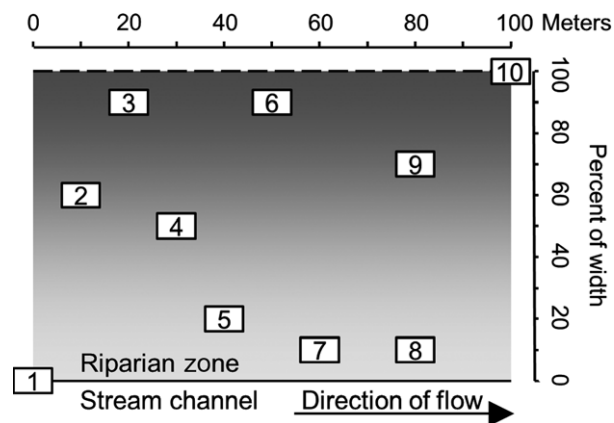
Fig. 2. Placement of plots within the riparian zones of study reaches. Plots were set up at a specific percentage of the riparian zone width away from the stream channel and at specific intervals along 100 m of the stream bank.

established a 1.0 m × 0.5 m plot, with the long side of the plot running parallel to the water front. Within each plot, we determined numbers of natural seedlings (i.e. natural in origin, not sown), and a set of habitat characteristics described below. We sowed seeds of six species directly adjacent to each plot.

Sowing

The six selected species differ in growth form and abundance in basic and enhanced reaches (Table 1). Before sowing, seeds were stored in cool, dark and dry conditions at 4 °C for 4 wk to break dormancy. Per species, an equivalent weight of 100 seeds (Table 1) was sown directly adjacent to the ten plots in each reach. After clearing away fresh debris and litter from the soil, seeds were sown in two side-by-side 5-cm diameter circles by gently pressing the seeds into the soil surface at the beginning of Jun 2014. To prevent confusion with natural seedling numbers in the plot, sowing locations were chosen so that the seeds had a very low likelihood of moving into the plot (e.g. by precipitation run-off). To ease seedling identification, seedlings with similar morphology were sown in different circles (Table 1). After 8 wk, the seedlings of experimentally sown species were identified and counted. Most of the experimentally sown species had similar germination in the field compared to optimal laboratory conditions, which suggests the germination period was sufficient. Since the count of sown seedlings after 8 wk is a result of both germination and establishment, we refer to it as recruitment.

Natural vegetation

The number of naturally occurring seedlings per plot was recorded during the vegetation surveys in Aug 2013 and 2014 to estimate recruitment from natural processes and sources. In the 2014 survey, the species of native seedlings were identified whenever possible, and the presence or absence of adults of that species within the plot was noted (for vegetation analyses see Nilsson et al. 2017).

Habitat characteristics

Soil moisture was measured for each plot in each reach using a ThetaProbe (Type ML2x; Delta-T Devices, Cambridge, UK) in Aug 2013 and in Jun, Jul and Aug 2014. We classified canopy (i.e. including everything higher than 40 cm) and litter cover per plot using four categories: 1 – none (<10%), 2 – little (10–50%), 3 – abundant (50–90%) and 4 – completely covered (>90%). We also determined riparian slope by measuring height and distance from the stream of the riparian border at nine locations and water level fluctuations with pressure loggers (Rugged TROLL 100; In-Situ Europe Ltd., Shirley, UK) during one full year.

In Aug 2014, three to five soil cores were taken per plot from the top 5 cm of soil and analysed for plant available N following the Devarda's method (protocol SS-EN 15476:2009; Swedish Standard Institute, Stockholm, SE), and plant available P after acid digestion with nitric acid (SS 028150-2) using ICP-AES. The soil organic content was determined by loss on ignition.

Geomorphic complexity of the reach

For eight of our 14 reaches, 27 geomorphic complexity parameters were measured by Polvi et al. (2014). These included quantification of variation in sediment distributions variation in reach plan-form and width, channel sinuosity and presence of in-stream wood (for details, see Appendix S1).

Data analysis

As reach restoration and geomorphic complexity act on larger spatial scales, we focused on reach-scale analyses. We summed the numbers of seedlings observed in the ten plots per reach and took the mean value per reach for each of the environmental variables. Categories of canopy and litter cover were converted to percentages by taking class means, and plot averages were calculated for soil moisture and canopy cover. The 90% flooding amplitude was calculated to represent maximum water level fluctuations, thus neglecting rare, extreme events.

The numbers of experimentally sown seedlings (per species and total of all six species), and the natural seedlings in 2013 and 2014 were compared between basic and enhanced reaches using a paired t-test to account for the paired layout of a basic and enhanced reach within each of

Table 1. Characteristics of the experimentally sown species.

Species	Growth Form	Abundance (%)		Ellenberg Moisture	100 Seed Weight (mg)	Sowed per Plot (mg)	Viability (%)
		Basic	Enh.				
Agrostis capillaris (Agr)[a,1]	Gras	6.8	13.6	5	9.4 (<0.1)	10	72.5 (3.0)
Carex acuta (Cx a)[b,2]	Sedge	0.3	0.3	9	93.8 (0.5)	90	1.5 (1.0)
Carex flava (Cx f)[b,1]	Sedge	16.9	6.2	9	118.5 (0.4)	120	1.0 (0.8)
Epilobium angustifolium (Epi)[b,2]	Herb	1.4	5.0	5	7.0 (<0.1)	10	3.8 (1.4)
Solidago virgaurea (Sol)[b,2]	Herb	17.3	37.5	5	42.4 (0.1)	40	18.9 (2.2)
Vaccinium myrtillus (Vac)[b,1]	Woody	37.0	15.6	6	24.4 (0.1)	30	45.5 (3.2)

Superscript numbers after the abbreviated species names indicates groupings in which seeds were sown in the field, and letters indicate the seed vendor companies. Abundance in the standing vegetation is indicated as summed vegetation cover in reaches with basic and enhanced (Enh.) restoration. Ellenberg moisture indicates the moisture affinity of the species, with higher numbers indicating preference for wetlands. 100 seed weight was calculated as the mean weight of five batches of 100 seeds. Seed weight sown per plot is the weight of seeds sown per plot (approximate equivalent of 100 seeds per plot per species). Viability is the mean count of experimentally sown seeds that germinated under laboratory conditions (moist soil and 22 $\pm$ 2 °C ($\pm$SD) on five replicates. SE are presented in parentheses.
[a]Obtained from Cruydt-Hoeck (Nijeberkoop, NL).
[b]Obtained from Jelitto Staudensamen (Schwarmstedt, DE).

the seven streams. A χ^2 test was used to determine whether there was a difference between basic and enhanced reaches in the frequency that natural seedlings and an adult plant of the same species co-existed at the same plot.

We performed a factor analysis on the geomorphic complexity measurements of Polvi et al. (2014) and our own abiotic measurements (organic material, canopy, litter, riparian slope, soil N and P concentrations). We extracted one factor that explained 32% of the variance. We inverted the complexity factor scores to make interpretation more intuitive (i.e. so that higher numbers indicate higher geomorphic complexity). We correlated total counts of experimentally sown (2014) and natural seedlings (in 2013 and 2014) to the calculated complexity factor. We tested the difference in complexity factor scores between restoration types with a paired samples *t*-test. All statistics were performed in IBM SPSS v 23 for Windows (IBM SPSS, Armonk, NY, US).

Results

Restoration and recruitment

After 8 wk, *Agrostis* and *Solidago* seedlings germinated in the majority of the plots in which they were sown (82% and 93% of all plots, respectively). *Epilobium* seedlings germinated in about half of the plots (54%), while *Carex acuta*, *Carex flava* and *Vaccinium* seedlings germinated in a lower fraction of plots (13%, 25% and 27%, respectively). Overall, 35.5 $\pm$ 2.7 ($\pm$SE) experimentally sown seedlings were observed per plot. Numbers of seedlings from experimentally sown species (individually and the total sum of all six experimentally sown species) per reach did not differ significantly between reach restoration types (Fig. 3) when tested with pair-wise *t*-tests (Appendix S2). On a small

scale, we observed slightly higher germination in plots of enhanced reaches for both *Carex* species and higher germination in the plots of basic reaches for *Vaccinium* (Appendix S2), but absolute differences were in the order of magnitude of just one or two seedlings.

Numbers of natural seedlings per plot ranged from 0 to 80 and from 0 to 64 in 2013 and 2014, respectively. They also varied considerably from 2013 to 2014, such that total seedling numbers per reach in 2013 and 2014 were not significantly correlated, nor were they significantly correlated to numbers of sown seedlings (Appendix S2). Although the summed number of natural seedlings per reach was twice as high in enhanced reaches compared to basic reaches in 2013, total summed number of natural seedlings did not differ significantly on a reach scale between reach restoration types (Fig. 3). In 2014, the numbers of seedlings in enhanced reaches decreased and were comparable to numbers observed in basic restored reaches (Fig. 3).
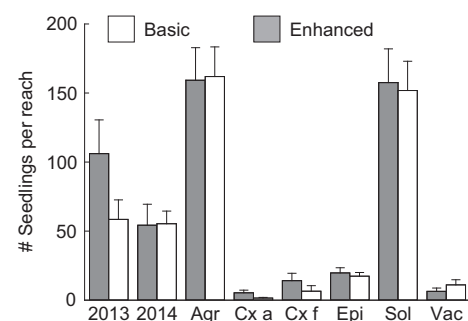
Fig 3. Average number of total seedling counts per species per reach 8 wk after sowing. See Table 2 for full species names. Error bars are SE, n = 7 for each bar.

Table 2. Correlation between the factor score for geomorphic complexity and habitat conditions (n = 8 for all).

	Type	Correlation	P-value
Stream Bed Slope		**0.955**	>0.001
P Concentration Soil (%)		**−0.861**	0.006
Fredle Index for Sediment Porosity (m)	V	**0.848**	0.008
Average Stream Bed Concavity (mm^{-2})		**0.808**	0.015
Mean In-stream Sediment Grain Size (cm)		**0.805**	0.016
Number of In-stream Wood Pieces		**−0.752**	0.031
Stream Bed Longitudinal Profile R^2	V	**0.747**	0.033
Sediment Heterogeneity of Small Sediment Fraction	V	**0.717**	0.045
N Concentration Riparian Soil (%)		−0.686	0.060
SD of Sediment Distribution (m)	V	0.646	0.084
Organic Matter (%)		−0.644	0.085
Sediment Coefficient of Variation (m^{-1})	V	−0.616	0.104
Total In-stream Wood Volume (m^3)		−0.612	0.107
Mean Riparian Soil Moisture (%)		−0.611	0.108
Coefficient of Variation of Reach Widths	V	−0.584	0.129
Sum of Errors of Deviation from a Gradual Stream Bed Slope	V	0.544	0.164
Coefficient of Variation of Water Depths	V	−0.537	0.170
SD of Reach Width (m)	V	−0.513	0.194
Spread in Sediment Distribution	V	−0.510	0.197
Stream Bed Longitudinal Sinuosity		−0.472	0.237
Mean of Errors of Deviation from a Gradual Stream Bed Slope	V	0.472	0.238
Sum deviations in Reach Width Scaled by Mean Width	V	−0.469	0.242
Mean Canopy Cover Riparian Zone (%)		−0.393	0.336
Bank Length Ratio Stream Bed	V	0.386	0.345
Longitudinal Roughness of the Channel (m)		0.372	0.364
Slope of the Riparian Zone		0.350	0.395
Longitudinal SD of the Channel (m)	V	0.342	0.407
Sediment Heterogeneity of Large Sediment Fraction	V	−0.305	0.462
Number of Side Channels		−0.298	0.473
Skewness of Sediment Distribution	V	0.275	0.510
Chain and Tape of the Channel Cross-section	V	0.247	0.555
Kurtosis of the Sediment Distribution	V	0.193	0.647
Average Reach Width Concavity (mm^{-2})		0.090	0.832
Litter Cover (%)		−0.068	0.874

Parameters describing in-stream variability of a certain geomorphic characteristics are indicated with a V. Bold indicates significant correlations.
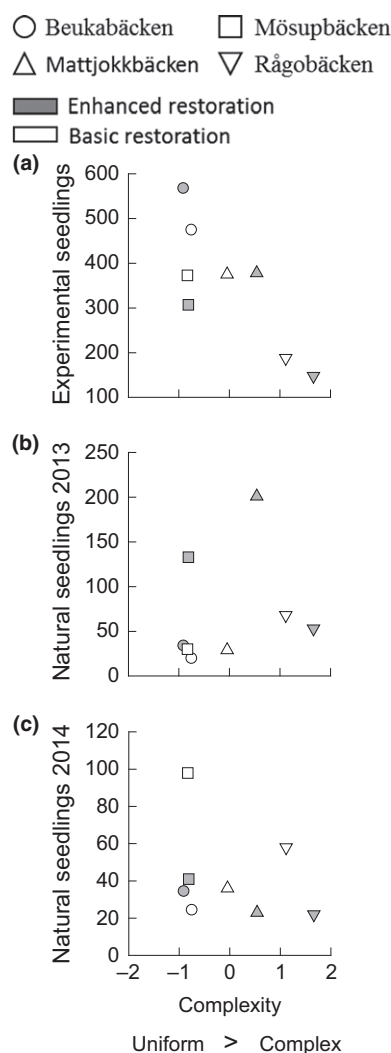
Natural seedlings were most often too small (<1 cm) to allow for species identification. Among the seedlings where identification was possible, *Potentilla erecta*, *Solidago virgaurea*, *Filipendula ulmaria* and *Betula* spp. were the most common (see Appendix S3). In 2014, for 71.8% of the positive identifications of natural seedlings, an adult individual of the same species co-existed in the same plot. This was the same for basic and enhanced reaches (72.5% and 70.9%, respectively; χ^2: 0.056, P = 0.814). For all identified natural seedlings, an adult plant of the same species was always found within the same reach, except for one *Achillea* seedling in an enhanced reach.

Geomorphic complexity

Based on the correlation of the individual parameters with the complexity factor scores (Table 2), it becomes clear

that more complex reaches had steeper slopes, larger grain sizes and porosity of in-stream sediment, and more nutrient-poor riparian zones. Our complexity factor scores further positively correlated to water level fluctuations (Pearson r = 0.706, n = 8, P = 0.05). However, although the complexity factor scores were somewhat higher in enhanced reaches compared to basic reaches, this was not significant for the four pairs of reaches (Paired samples t-test, t = −1.324, df = 3, P = 0.277).

The numbers of experimentally sown seedlings of a reach were correlated significantly to the complexity factor scores (Pearson r = 0.82, P = 0.013; Fig. 4a). Looking at the sown species individually, the negative relationship between recruitment and complexity factor scores was significant for *Agrostis*. The other species had consistent (except for *Epilobium*), but not significant relationships (Table 3). Counts of natural seedlings per reach were

Fig. 4. Relationships between complexity factor scores and numbers of seedlings from experimentally sown species (**a**), from natural seedlings in 2013 (**b**) and 2014 (**c**).

Table 3. Correlations between seedling numbers and complexity factor scores.

	n	Pearson r	P
Agrostis capillaris	8	**−0.945**	**<0.001**
Carex acuta	8	−0.272	0.515
Carex flava	8	−0.534	0.173
Epilobium angustifolium	8	0.212	0.615
Solidado virgaurea	8	−0.540	0.168
Vaccinium myrtillus	8	−0.423	0.297
Natural seedlings 2013	8	0.211	0.616
Natural seedlings 2014	8	−0.283	0.497

Bold indicates significant correlations.

Complexity and recruitment

For our first hypothesis, we assumed that higher geomorphic complexity would improve habitat suitability for recruitment, so we expected increased recruitment of sown seeds in enhanced reaches compared to basic reaches and a positive relationship between geomorphic complexity and recruitment. We found no clear effect of restoration on recruitment, but since we also did not observe a clear increase in complexity factor scores in enhanced reaches, it remains inconclusive whether increasing geomorphic complexity with restoration can increase recruitment of sown or natural seeds. Even though the differences between basic and enhanced restoration are of smaller magnitude than those between channelized and basic restoration, several authors have indicated that enhanced restoration can significantly increase geomorphic complexity (Polvi et al. 2014), decrease flow velocities (Nilsson et al. 2017) and increase flooding duration and frequency (Kuglerová et al. 2016). Despite all the restoration work, we did not detect a significant effect of these activities on either complexity factor scores or recruitment. This may be due to the difference being minor or to methodological limitations, such as the number of replicates.

Despite the lack of pair-wise differences between basic and enhanced reaches, there was quite a lot of variation in geomorphic complexity between all reaches. This spread of variation between all reaches can provide insight into how a large range of geomorphic complexity may affect recruitment, more so than by using the small (and non-significant) pair-wise differences between basic and enhanced reaches. The large variation in the reach complexity gradients is likely based on landscape settings, as can be seen in the correlation of landscape factors with the complexity factor. In contrast to our hypothesis, however, we found that reaches with higher geomorphic complexity had lower recruitment from sown seeds. This is unexpected, as previous studies provide evidence for the importance of geomorphic complexity and associated flow regime for recruitment. Restoration of channelized reaches, for

not significantly related to the complexity factor score (Fig. 4b, c), either in 2013 or in 2014 (Table 2).

Discussion

We did not observe differences between restoration types in numbers of sown and natural seedlings, nor did we find a clear difference in complexity between those reaches. Highest recruitment of experimentally sown seeds occurred in reaches with gradual slopes, small sediment grain sizes and high nutrient concentrations. However, numbers of natural seedlings varied strongly between 2013 and 2014 and were not related to the complexity factor scores. Potential parent plants of natural seedlings occurred frequently at a very local scale, and this frequency did not differ between restoration types.

instance, has been shown to increase sunflower survival, although germination was not affected (Dietrich et al. 2015). Additionally, Jansson et al. (2005) pointed towards the clear importance of factors that increase flooding, as their flooded plots were colonized more frequently by new seedlings compared to non-flooded plots. However, on larger spatial scales, colonization differences between regulated and unregulated rivers in Jansson et al. (2005) were absent, even though the streams had distinctly different flooding regimes. Our study contrasts with these findings as we found highest recruitment in reaches that had smaller complexity factor scores and smaller water level fluctuations. These often somewhat ambiguous results show that we do not fully understand the interactions between geomorphic complexity, flow regime and recruitment.

Geomorphic complexity is thought to enhance recruitment by providing more heterogeneous micro-habitats in which different species can find suitable recruitment conditions (Fraaije et al. 2015a). This would result in a positive relationship between complexity factor scores and recruitment, but instead we found a negative correlation. One explanation could be that our selection of species, even though they represented a wide range of habitat preferences, had similar recruitment conditions and was therefore too narrow to achieve this effect of niche availability. Indeed a growing body of authors argue that most species have identical recruitment requirements (Lenssen et al. 1998; Boedeltje et al. 2002; van Leeuwen et al. 2014) and only specific species show niche specialization during germination. If so, increasing reach heterogeneity would not increase recruitment, but instead could result in a negative relationship between recruitment and geomorphic complexity if the more homogenous reaches have more suitable recruitment conditions. The observed negative relationship between recruitment of our selection of species and complexity factor scores thus suggests that the habitat conditions in less complex reaches were generally more suitable for recruitment of those species compared to those with higher geomorphic complexity. Since we found similar trends between species, we assume that the observed trends may be extrapolated to natural seedling communities despite our use of non-local seeds. This seed origin could merely have resulted in less than optimal performance in some species, but would likely not have affected patterns. We added a high number of seeds per species to overcome potentially overall lower germination due to poor adaptation of the non-local seeds.

Complexity and environmental conditions

Geomorphic complexity is thought to affect habitat condition mostly indirectly via its effects on the flooding regime, sedimentation and retention processes. Our results indeed point towards a clear relationship between geomorphic complexity and water level fluctuations, which is in line with other studies (Kuglerová et al. 2016; Nilsson et al. 2017). This could result in indirect effects on habitat quality and, additionally, in differences in seed input through dispersal (Fraaije et al. 2015b).

Besides an effect on water level fluctuations, we observed strong relationships between our complexity factor and soil quality (sediment grain size and nutrient content), with complex reaches having on average larger-sized sediment and lower concentrations of soil organic matter and nutrients (N and P). This finding is in line with the differences between simple, channelized reaches and basic restored reaches reported in previous studies (Dietrich et al. 2014, 2015; Hasselquist et al. 2015; Kuglerová et al. 2016). Though somewhat counter intuitive, our findings are also in line with hydromorphic theories that predict that with decreasing stream slope (thus decreasing complexity), water flow decreases, allowing more fine sediment and organic particles to settle. It has therefore to be noted that any type of restoration of geomorphic complexity will restore the complexity within the landscape-scale settings such as slope, and restoration should not aim to exceed this just because more geomorphic complexity is desired.

Previous studies suggest that soil organic matter content and sediment grain size can influence germination and early seedling growth by affecting soil moisture, since smaller grain sizes and higher soil organic content have a higher capacity to retain water (Keddy & Constabel 1986). However, results of this study suggest that nutrient availability (of the organic material) could also play a role, as we observed that both recruitment from sown seeds and soil nutrients were related to the complexity factor scores. Although boreal riparian zones characteristically have low nutrient levels, restored reaches generally have somewhat higher nutrient concentrations compared to channelized reaches (Dietrich et al. 2014; Kuglerová et al. 2016). Our results imply that increased recruitment due to higher availability of nutrients may be a mechanism that led to the in the increase in species richness that Helfield et al. (2007) and Kuglerová et al. (2016) observed after restoration. In addition, the strong negative relationship between channel slope and reach species richness observed by Hasselquist et al. (2015) could be due to the suitability of the habitat for recruitment, given that our study found a correlation between both slope and recruitment of sown seeds and complexity factor scores (i.e. less complex streams with more gradual slopes also had higher recruitment).

Complexity and dispersal

Assuming that recruitment patterns observed in our experimentally sown species, despite the seeds being obtained from vendors, were representative of the recruitment in a community of natural species, we hypothesized in our second hypothesis that if dispersal was uniform at all reaches, there would be a correlation between sown seedlings and natural seedlings. If this were the case, less complex reaches would have higher recruitment of natural seedlings compared to more complex reaches, similar to the observation for experimentally sown seeds. Instead, we found no correlation between the two seedling types and no relationship between geomorphic complexity and natural seedling numbers. This may therefore suggest that dispersal limitations counteracted the effects of the improved recruitment conditions observed in the less complex streams.

A direct test to quantify dispersal was not performed, but two pieces of evidence indicate that dispersal limitations were present. First, as explained above, geomorphic complexity was correlated with sown seedlings but not with natural seedlings. Second, roughly 70% of the natural seedlings that could be identified had a potential parent plant nearby. As a result, we reject our third hypothesis, which was that enhanced reaches would allow more seed deposition of long-distance dispersed seeds via hydrochory, and therefore have a lower proportion of natural seedlings with a potential parent plant nearby compared to reaches with only basic restoration. Interestingly, however, the only identified natural seedling for which no potential parent plant could be found within the reach was observed in an enhanced reach. This is in line with our third hypothesis, although the fact that it was only observed once further supports the existence of dispersal limitations.

In conclusion, this study provides some evidence supporting the idea that dispersal and seed deposition is increased with geomorphic complexity, although enhanced restoration itself may not have resulted in a strong enough increase in geomorphic complexity to change recruitment (Andersson et al. 2000; Gurnell et al. 2008; Nilsson et al. 2010). However, it remains to be investigated whether higher seed retention on longer temporal scales will result in higher species richness, as suggested in the study of Andersson et al. (2000). Alternatively, the strong dispersal limitations and the negative relationship between geomorphic complexity and recruitment habitat could have a stronger effect than dispersal on species richness, leading to the negative correlation between slope and richness, as observed by Hasselquist et al. (2015). Further, the high variability of natural seedling numbers between 2013 and 2014 suggest that additional external factors, such as wave action or herbivory, may decouple the relationship between stranding and diversity (Sarneel & Soons 2012; Veen et al. 2013).

Implications

Our study shows that recruitment can limit vegetation development. We found that recruitment differences were minor between reaches that differed in the degree to which geomorphic complexity was restored, but that steep reaches with large mean sediment size are less suitable for recruitment compared to less complex sites with more gradual slopes, less coarse stream sediment and higher nutrient concentrations in the riparian soil. However, this does not imply that increasing geomorphic complexity with restoration may impede recruitment. In fact, restoration decreases flow velocities and generally increases the abundance of finer sediment fractions that can be deposited during flooding in the riparian zone. Understanding how processes (e.g. environmental filtering, dispersal, recruitment and plant growth) are affected by different methods of restoration and how they relate to geomorphic complexity in general is important, and nature managers should therefore take into account the general geomorphic settings when appraising the effects of restoration. The indications that restored reaches in general (still) suffer from dispersal limitation may suggest that catchment-scale restoration and increased connectivity between dispersal sites are important measures that could magnify vegetation changes resulting from restoration work.

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Supporting Information

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

Appendix S1. Geomorphic complexity.
Appendix S2. Statistics at a plot level.
Appendix S3. Species identity of natural seedlings.