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RESEARCH ARTICLE

River restoration effects on dispersal and the development of riparian seed bank: do poor seed banks limit restoration of boreal riparian zones?

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In boreal streams, restoration after channelization typically consists of increasing instream geomorphic complexity with no other active restoration measures (e.g. planting) as it mainly targets fish. Unsurprisingly, this restoration fails to restore riparian vegetation within the time frames needed to meet biodiversity goals. To understand the potential role of dispersal and seed banks in the poor restoration results, we compared deposition patterns from a seed release experiment conducted during spring flood and summer low flow conditions to seed bank- and vegetation composition. The experiment was conducted across seven boreal streams, each differing in time since restoration (0–22 years). We found that seed deposition increased due to low flow and local flow obstruction, suggesting the importance of instream boulders. Locations where there was a high deposition likelihood in our seed release experiment had higher Shannon diversity compared to locations with a low seed deposition likelihood. Riparian vegetation composition is related to flow obstruction, while seed bank species composition is correlated to spring flood seed deposition. In general, the sampled riparian seed banks contained few seeds and species. We therefore conclude that (1) restoration of hydrogeomorphic complexity (especially instream boulders) can enhance seed deposition with some effects on species composition of the vegetation and seed bank diversity, and (2) the importance of these generally species poor seed banks for the return of species after restoration boreal streams is questionable. Other (active) methods or more time may therefore be needed to meet biodiversity goals within riparian vegetation restoration.

Key words: boreal seed bank formation, geomorphic complexity, hydrochory, plant seed dispersal, riparian vegetation diversity, seed release experiment, stream restoration chrono sequence

Implications for Practice

- It is unlikely that seed banks will significantly contribute to local plant diversity after restoration of boreal riparian vegetation, as they were small and unrelated to the standing vegetation. Instead, active planting or seeding or measures enhancing seed dispersal may be required.
- Careful, fine-scale planning of the boulder placement and flow velocity distribution could aid riparian vegetation restoration of boreal riparian zones, as boulders in the direct vicinity of the bank and low flow conditions enhanced seed deposition and related to species composition of the riparian vegetation.
- Since seed banks contained species that are not found in the vegetation, they could potentially contribute to landscape-scale biodiversity.

Introduction

Riparian zones are biodiversity hotspots in the landscape. Additionally, they receive and filter water, transport sediments and nutrients from upslope areas, and thus provide critical ecosystem services (Naiman & Décamps 1997; Gundersen et al. 2010). Despite their importance, numerous restoration projects, protective policies, and regulations (e.g. EU Water Framework Directive) have failed to meet goals to improve natural water flows and increase species diversity, habitat quality, and connectivity (Hasselquist et al. 2015; Nilsson et al. 2015). Many restoration actions target habitat structure and flow regimes, assuming that species and ecosystem functioning will follow (i.e. “Field of Dreams hypothesis,” Palmer et al. 1997). In boreal zones, these passive restoration approaches that restore hydrogeomorphic

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complexity of the streams (replacing boulders back into channelized streams) are more common compared to active restoration approaches of the riparian zone (e.g. planting or sowing). Consequently, the lack of success in restoration of riparian biodiversity is often attributed to limited propagule dispersal.

Hydrochorous dispersal of plant propagules via water is considered the main dispersal vector for riparian zones in boreal streams, while wind and animal dispersal play a minor role in maintaining riparian biodiversity (Merritt et al. 2010; Nilsson et al. 2010). Almost all plants that grow close to the water are characterized by seeds and vegetative propagules that float well (Nilsson et al. 2010; Sarneel 2013). Additionally, propagules of riparian species have been shown to travel over hundreds of kilometers (Andersson et al. 2000; de Jager et al. 2019; Su et al. 2019), and enormous numbers of seeds have been trapped in flood-deposited drift material, collected in rivers of various sizes (Boedeltje et al. 2004; Vogt et al. 2004; Osunkoya et al. 2014). Therefore, it has been assumed that flood events are crucial in providing riparian zones with new propagules. As such, restoration of hydrogeomorphic complexity, like boulders that will enhance flooding frequency, is thought to benefit seed dispersal to riparian zones and thus contribute to the restoration of the riparian zone. However, other studies have found no, or very weak, overlap between deposited seed composition and vegetation composition (Andersson et al. 2000; Merritt & Wohl 2006), challenging the dominant role of flooding as a seed source for vegetation recovery after restoration in boreal systems.

Instead, or in addition to dispersal, the soil seed bank could be an important seed source that influences riparian plant community development after restoration. Yet, little is known about the role of riparian seed banks in restoration. This contrasts with, for instance, grassland restoration, where seed banks are frequently studied to assess their potential contribution to restoration (Kiehl et al. 2010; Kiss et al. 2018). From these grassland studies, we know that species dominating before restoration are abundant in the seed bank, but the seed bank can also include new species. Furthermore, successional patterns in the vegetation after restoration or land abandonment are matched by changes in the seed bank (Wienhold & van der Valk 1989; Yamada et al. 2013).

Studies of riparian seed banks show that seed densities can be quite variable in space, ranging from 260 to 61,090 seeds/m^2 (Bakker et al. 2013; Osunkoya et al. 2014; Greulich et al. 2019), as well as over time due to sediment deposition or erosion (Lee et al. 2014; O′ Donnell et al. 2014). Two previous studies suggest that differences in flooding duration could account for some of the spatial variation in seed bank species richness in the floodplains of the Three Gorges River (Chen et al. 2019) and a newly created channel in the river Cole (Gurnell et al. 2006). Both studies suggest considerable proportions (20.4%; Chen et al. 2019) of the seeds and species (50%; Gurnell et al. 2006) within the seed bank were the result of direct deposition by hydrochory, indicating that this process plays a key role in seed bank formation. Despite this, we currently lack understanding of (1) the processes forming riparian seed banks, (2) their potential to assist the recovery of riparian plant communities after restoration in boreal streams, and (3) the long-term importance of seed banks for restoration.

In the otherwise relatively undisturbed boreal streams in Fennoscandia, streams were channelized during the timber-floating era (1850–1950; Nilsson et al. 2005) by pushing boulders to the stream banks, cutting off side channels, and creating levees that disconnected the riparian zones from the stream. Restoration typically consists of returning the boulders and adding dead wood to the stream, re-widening the channel, and re-opening side channels without any further active measures (described in detail in Gardeström et al. 2013). Hence, directly after restoration measures, the riparian zones are covered with established perennial vegetation that is adapting to new soil moisture and flooding conditions and smaller patches of bare soil (e.g. from machine driving, root wads of felled trees, and bolder removal). Restoration of the geomorphic structural complexity increases the variation in the speed and direction of the stream flow (Gardeström et al. 2013; Polvi et al. 2014). This, together with the addition of structures that trap seeds (e.g. large wood), has been shown to result in a larger deposition of seed (mimics) dispersed by water (Engström et al. 2009; Su et al. 2019). Although this increases the forb diversity somewhat after greater than 15 years of restoration (Hasselquist et al. 2015), the response of the riparian vegetation is in general limited (Nilsson et al. 2017). To understand why there is such poor restoration of biodiversity, we studied the seed bank as a potential source for vegetation recovery, as well as the relationship between seed banks and spatial variation in seed deposition via hydrochory. These studies were conducted in seven stream reaches where the hydrogeomorphic complexity was restored, while no other restoration activities have been carried out to improve the riparian habitat.

First, because restoration of hydrogeomorphic complexity affects hydrochory, we hypothesized that spatial patterns of seed deposition across and within streams are related to hydrogeomorphic characteristics (e.g. the number of boulders, flow, channel slope, and bank morphology). Second, if spatial variation in hydrochory drives riparian seed bank composition, we hypothesize that locations where seeds are more likely to be deposited have higher numbers of seeds and more diverse seed banks compared to locations where seeds are less likely to be deposited. Third, if seed banks are important for the restoration of vegetation in boreal riparian zones, we hypothesized a high similarity between the species composition of the seed bank and the vegetation. Fourth and lastly, the similarity in species composition between the seed bank and the vegetation was hypothesized to decrease with time after restoration, as we expect that vegetation recovery initially may depend on the seed bank as they are the first available seed source after restoration (Weidlich et al. 2021). With time, continuous hydrochorous seed input may change the seed bank; however, because the standing vegetation may hamper recruitment from the seed bank, the similarity between vegetation and seed bank may decrease.

Methods

To study the relationship between restoration of hydrogeomorphic complexity, the probability of seed deposition, and seed bank and riparian vegetation composition, we selected seven reaches of streams with differing time since restoration in the Vindel River catchment of northern Sweden (WGS84 between 64.8, 18.4 to 65.6, 16.8 and 280 to 480 above the current sea level; Fig. 1). In each stream reach, we experimentally determined the patterns of seed deposition likelihood in May and August 2017. We analyzed the seed bank content using a seedling emergence test (Ter Heerdt et al. 1999) of 12 plots per reach that had contrasting seed deposition and conducted vegetation surveys at each plot where seed bank samples were taken.

Location Description

The Vindel River catchment is located in the boreal zone. The riparian vegetation of Vindel River tributaries (average riparian width: 8 m) is characterized by sedges and grasses (e.g. *Carex flava* L. and *Molinia caerulea* [L.] Moench), mixed with forbs (e.g. *Potentilla erecta* [L.] Raeusch. and *Solidago virgaurea* L.), close to the river channel. At higher elevations, further from the stream, dwarf shrubs dominate (e.g. *Vaccinium* sp. and *Calluna vulgaris* [L.] Hull) that soon transition to typical boreal coniferous forest with *Maianthemum bifolium* (L.) F. W. Schmidt, *C. globularis* L., and *Pyrola* sp. in the understory. The flow regime is characterized by a large spring flood (Fig. S1), occurring directly after snowmelt from late May to early June, raising the water table in our stream reaches on average 34.4 cm (Table S1). Floods during autumn and winter are usually shorter in duration as they occur after rain events and ice jams, respectively (Fig. S1). We selected six restored reaches, with varying time since restoration, and one channelized reach. They all share a history of channelization due to timber-floating practices (see Nilsson et al. 2015 for a detailed description). Restoration has been ongoing since the late 1980s and consists of increasing stream channel geomorphic complexity without active restoration of the riparian zone (Hasselquist et al. 2015). For details on how restoration increased hydrogeomorphic complexity and affected

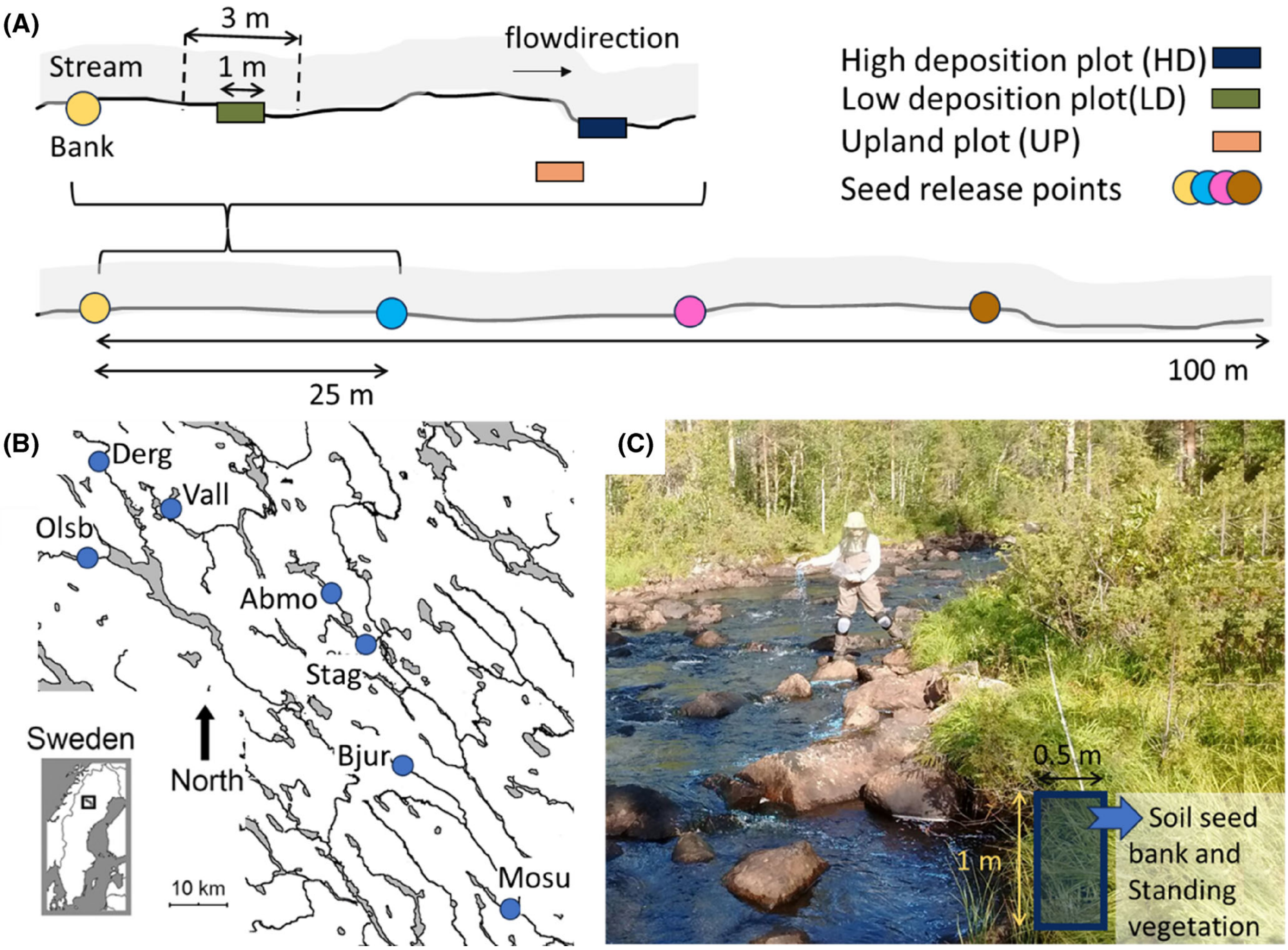

Figure 1. Sampling design. (A) Schematic overview of sampling per reach with the four release points of seeds (circles) and an example seed bank plots (rectangles) for one of the four 25 m sections. (B) Map of the seven study reaches, indicated by blue circles with the stream name abbreviation and time since restoration, in years at the time of the study. Black lines indicate rivers, and gray indicates lakes. The few roads that run through the area are not shown. Modified from www.eniro.se. Abmo = Abmobäcken, Bjur = Bjurbäcken (channelized), Derg = Dergabäcken, Mosu = Mosupubäcken, Olsb = Olsbäcken, Stag = Stagtraskbäcken, Väll = Vällingträskbäcken. (C) Example of a restored reach (Abmobäcken in August) just after seeds being released, indicating plot size and the parameters measured per plot.

riparian plant species, see Gardeström et al. (2013), Polvi et al. (2014), Hasselquist et al. (2015), Kuglerová et al. (2016), and Nilsson et al. (2017).

Seed Deposition Experiment

To study if hydrogeomorphic complexity affects hydrochory, we compared spatial patterns of the seed deposition likelihood across and within streams and related these patterns to stream geomorphology. We performed a hydrochory seed release experiment using sterilized sunflower seeds (Andersson et al. 2000; Engström et al. 2009) and determined the seed deposition likelihood from those results as an alternative to measuring the deposition of natural seeds. This standardized the variation of seed availability across time and space. In each reach, we marked a transect of 100 m. Starting upstream of this transect, we released 0.5 kg of colored sunflower seeds (circa 9000 seeds) at four 25 m intervals (Fig. 1). We used a different color at each release point, and the releases occurred shortly after each other. One hour after the sunflower seeds were released, we counted the number and color of seeds deposited at each meter of riverbank, starting 105 m downstream from the first release point and ending 5 m upstream from the first release point (to control for potential upstream dispersal). We also timed the fastest sunflower seeds over the first 10 m after each release in each 25 m interval. We refer to this as release speed. Based on the release speeds, a 1 hour waiting time would have allowed the fastest seeds to travel on average 3.9 ± 0.5 km in May and 2.1 ± 0.5 km in August. Counting the entire reach was usually completed within 4 hours. We performed the experiment twice in each reach, once at peak spring flood conditions in May and once during low flow in August (Fig. S1) of 2017, which was an average year in terms of discharge (Swedish Meteorological and Hydrological Institute 2017). While we are aware that our methodology can result in an underestimation of absolute dispersal distances, the measured seed deposition patterns are likely to correlate to deposition patterns after longer time periods (e.g. 24 hours), and to those of natural seeds (Bång et al. 2007; Engström et al. 2009). Hence, we considered the patterns of trapped sunflower seeds to reflect the seed deposition likelihood.

After the sunflower release experiment, we established 12 study plots in each reach. To this end, we selected four 0.5 m^2 plots in bank sections with a high seed deposition likelihood (HD plots) and four 0.5 m^2 plots in sections with a low seed deposition likelihood (LD plots). HD and LD plots were both at the waterline, and the distinction between them was based on the sunflower seed release experiment in May. That is, we classified a 3-m section with above average seed deposition per meter (with the study plot in the center) as HD and below average as LD. Four additional plots (UP plots) were selected upland, at higher levels, from the HD plots (Fig. 1). Those UP plots were located between the spring flood limit of that year (measured with water loggers, see below) and the upland riparian border. The upland riparian border was determined by the maximal spring flood height and is indicated by a sudden increase of dwarf shrubs (*Vaccinium* spp.). Plots measured 1 × 0.5 m with the long edge parallel to the water line. To spread the HD, LD, and UP plots across the reach, we selected one HD, LD, and UP plot in every 25 m section of each reach, excluding the first 5 m after the release point (Fig. 1). These 5 m were excluded as high seed deposition within this section was most likely determined by sunflower seed density rather than this section featuring ideal characteristics for seed deposition.

Seed Bank Analysis

Directly after the spring flood, in early June 2017, we collected a seed bank sample from each HD, LD, and UP plot in each reach ($12 \times 7 = 84$ samples). Each plot was sampled by taking six 4 cm deep soil cores with a 2.5 cm diameter root auger. The six cores from each plot were combined and then transported in cool and dark conditions to the greenhouse facilities at the Swedish University of Agricultural Sciences (SLU), in Umeå, Sweden. Roots and occasional stones were removed, after which each sample was spread as a thin layer on top of a 5 cm deep standard soil layer in a 20 × 20 cm plastic tray. The standard soil layer consisted of a mixture of two parts potting soil (K-jord, Hasselfors garden, Örebro) and one part sand (Boke International AB, Kvänum). The trays were placed in a plastic greenhouse on the 21st of June 2017. The mean daily temperature inside the unheated greenhouse was 18.4 ± 0.4°C SE, which was an increase of 3.5°C compared to long-term mean temperature in July and August (Swedish Meteorological Institute, SMHI). At the start of autumn, in mid-August, the trays were placed in a climate room where they were kept at a 16-hour light regime (approximate light intensity 115 μmol/s) at 20.9 ± 0.08°C SE until the fourth of May 2018. Trays were watered at least twice per week, and germinated seedlings were counted, removed, and determined to species level (Mosberg & Stenberg 2010) at least once a month. When necessary, seedlings were transplanted to separate pots for a few weeks to develop further until species determination was possible.

Vegetation Survey

In August 2017, species composition was determined in each 0.5 m^2 plot in which the soil seed bank was sampled (12 per reach). We scored species abundance on a scale of five classes (1: rare, one individual, 2: less than 5% cover, 3: 6–25% cover, 4: 26–50% cover, 5: more than 50% cover). The presence of water and bare ground were scored using the same classes. Additionally, we counted the number of flower heads per plot as a measure of potential seed input by the local vegetation.

Hydrogeomorphic Survey

To measure the spring flood height (cm), we placed a water logger (Rugged Troll 100, In-Situ Inc., Fort Collins, CO, U.S.A.) in the stream channel and an associated barometric pressure logger in each reach in October 2016. Additionally, we measured channel velocity (m/s) in the channel center at five points evenly distributed along the reach (em-flow meter model 801, Valeport Limited, Devon, U.K.). To obtain a mean channel velocity for each study plot (V_c), we averaged the two measurements at the upstream and downstream ends of the 25 m section in which the study plot was located. We weighed the average by the distance to the measurement. We further used release speed as a measure of surface water velocity at each seed release point by measuring the time that the fastest sunflower seed needed to disperse over 10 m after their release. To capture geomorphology, we counted the total number of boulders protruding from the water surface in each 25-m section of each reach in May and August. For each 1-m bank section, we determined bank form (straight, concave/bending into the bank, convex/bending into the water, pools, or more complex), the presence or absence of a flood mark (e.g. deposited material) and flow obstruction close to the bank. We considered the flow to be obstructed when boulders, vegetation, or dead wood protruded from the water within 1 m of the bank, thus causing deviation from the longitudinal surface water flow (i.e. either obstructed or not). Last, we measured channel width and riparian width at the location of each plot, using a Trimble S3 total station.

Calculations

Total numbers of deposited sunflower seeds per reach were calculated as the sum of the number of counted sunflower seeds from all four release points. We calculated cumulative dispersal curves based on the numbers of deposited sunflower seeds from the first, most upstream release point in each reach. We also calculated the distance over which the first cumulative 250 sunflower seeds were deposited as a measure of dispersal distance. We further quantified the local seed deposition likelihood for each HD and LD plot (0.5 m^2) by dividing the number of deposited sunflower seeds by the total number of sunflower seeds that were still in the water (i.e. the total number of released seeds subtracted from the number of seeds already deposited upstream). To quantify more broad deposition patterns, we summed all the counted seeds from a 3 m section surrounding the plot and summed all the sunflower seeds deposited in that 25 m section of the color that was released in that reach section.

We calculated the fraction of different plant functional groups (herbaceous, grasses, and woody species) and the Shannon diversity index (Good 1953) separately for the seed bank and the vegetation of each study plot. As deposition patterns of sunflower seeds substantially changed between May and August, we excluded HD and LD plots that had high seed deposition in 1 month (classifying as HD) and low sunflower deposition (classifying as LD) in another month. Instead, we focused on the 19 HD plots with consistently high (above average in May and August; including all reaches) and 18 LD plots with low sunflower seed deposition (below average in both months; excluding one reach).

Statistical Analysis

We used beta-regression to test if the seed deposition likelihood per square meter of seeds released at the start was affected by month and the longitudinal distance from the release point as predictor variables. A random factor that nested reach within a month accounted for the repeated measurements over time (Cribari-Neto & Zeileis 2010). To specifically test if differences in flow velocity could account for the differences between months, we tested a linear mixed model with total number of seeds deposited per 25 m as the dependent variable and release speed and month as independent variables. A random factor nesting a 25-m section within reach was added. To test the effect of bank form, the deposition likelihood per square meter on different bank forms was averaged for each bank form in each 25-m reach section to prevent bias due to overrepresentation of a certain bank form in a reach ($n =$ maximally 4 per reach). Except for pools, all reaches contained all bank forms in May, while in August only two reaches lacked one of the bank forms. We used beta-regression with bank form (straight/concave/convex/complex), month (May/August), and flow obstruction (present/absent) as predictors and 25 m section nested in reach as the random factor to acknowledge the nested sampling structure. Post hoc testing was done using the emmeans package (Lenth et al. 2023).

We tested how HD, LD, and UP plots differed in their species numbers and the Shannon diversity index of both their seed bank and vegetation separately. For this, we used four linear models (one for each diversity characteristic) that included plot type as an independent variable and reach name as a random factor. We excluded *Gymnocarpium dryopteris* (L.) Newman and *Phegopteris connectilis* (Michx.) Watt from our analysis since these species dominated the seed bank composition in two streams (Table S2), contributing to more than 90% of the "seedlings" that appeared. Including those species would have masked general patterns and revealed patterns for these species only.

To assess community composition differences between the riparian vegetation and seed bank and between HD, LD, and UP plots, we used nonmetric multidimensional scaling ordination (NMDS). We converted seed counts and cover estimates to standardize them as proportions of the study plot total seed count or summed cover. We used the *metaMDS* function in the *vegan* package (Oksanen et al. 2018) to perform the NMDS analyses. We used Bray–Curtis dissimilarities to project the species composition data onto ordination space. To determine the statistical differences among groups in NMDS space (seed bank vs. riparian vegetation or HD, LD, and UP plots), we conducted permutational multivariate analyses of variance (PERMANOVA) for each NMDS analysis using the *adonis* function in the *vegan* package (Oksanen et al. 2018). When significant differences were found, we used a post hoc *pairwise.adonis* (Martinez Arbizu 2020), adjusting for multiple comparisons using a Bonferroni correction. We used the function *envfit* within the *vegan* package (Oksanen et al. 2018) to determine if the species composition in the seed bank and riparian vegetation related to the total seed deposition at a 3 and 25 m scale, geomorphology (number of boulders, channel width, riparian zone width channel velocity, and release speed), local seed production (number of flower heads per plot), or time since restoration. Except for the last two, all variables measured in May and August were added separately. This provided correlation coefficients and p values for each reach characteristic and hydrogeomorphic variable with the plant and seed species composition data.

To find indications of links between seed deposition patterns and seed bank content, we ran an explorative set of correlations as we felt that a stepwise regression would lead to overfitting of our data. To this end, reach characteristics, including time since restoration, the total number of deposited sunflower seeds (100 m) in May and August, and the summed number of seeds in the seed bank per reach, were correlated with the total number of seeds in the seed bank and the total species richness in the seed bank (including only the LD and HD plots since those were at the water line). In addition, the Bray–Curtis dissimilarities were calculated for the comparison between the vegetation and seed bank of each plot, the plot vegetation within a reach and the seed bank composition within a reach. Using the mean per reach, those dissimilarities were also correlated to time since restoration, the total number of deposited sunflower seeds (100 m) in May and August, and the summed number of seeds in the seed bank per reach.

Results

Spatial Seed Deposition Patterns

The numbers of sunflower seeds per 25 m section decreased significantly with increasing release speed (beta-regression $\chi^2 = 12.2$, $p < 0.001$), but no interaction was found between month and release speed (beta-regression $\chi^2 = 0.017$, $p = 0.895$; Table S3). Over the 100-m long reach, the cumulative number of deposited sunflower seeds increased relatively stepwise, with sections in which many or few seed mimics were deposited (Fig. 2A & 2B). The seed deposition likelihood per meter (Fig. 2C) was lower in May than in August (beta-regression $\chi^2 = 41.00$, $p < 0.001$; Table S4), but did in general not exceed 3% of the total number of released seeds. No interaction with distance from the release point was found, showing that the decrease with distance was similar in both months (beta-regression $\chi^2 = 0.050$, $p = 0.823$).

Of the sunflower seeds released at the reach start, the highest deposition likelihood was found in pool sections. However, pools occurred infrequently, and hence their replication was too small to add them as a bank form category. Concave and complex bank forms had the highest (especially in August) and convex bank forms the lowest seed deposition likelihood per square meter (especially in May), but these differences between bank forms were not significant (beta-regression $\chi^2 = 7.46$, $p = 0.059$; Tables S5 & S6). Neither the effect of month (beta-regression $\chi^2 = 1.64$, $p = 0.200$) nor the interaction between month and bank form (beta-regression $\chi^2 = 6.63$, $p = 0.085$) flow obstruction significantly increased the seed deposition likelihood (beta-regression $\chi^2 = 4.44$, $p = 0.035$). This effect was strongest in August (Table S6; Fig. 3), with a significant interaction between flow obstruction and month (beta-regression $\chi^2 = 3.97$, $p = 0.046$; Tables S5 & S6; Fig. 3). The three-way interaction was not significant, indicating that obstruction and month affected the seed deposition likelihood per square meter similarly for all bank forms (beta-regression $\chi^2 = 0.283$, $p = 0.963$). For other interactions and post hoc contrasts, see Tables S5 and S6.

Riparian Seed Bank and Vegetation Composition

Per seed bank sample, on average 87.8 ± 15.8 SE seedlings and 5.55 ± 0.23 SE species germinated, equaling 29,805 seedlings/m^2.

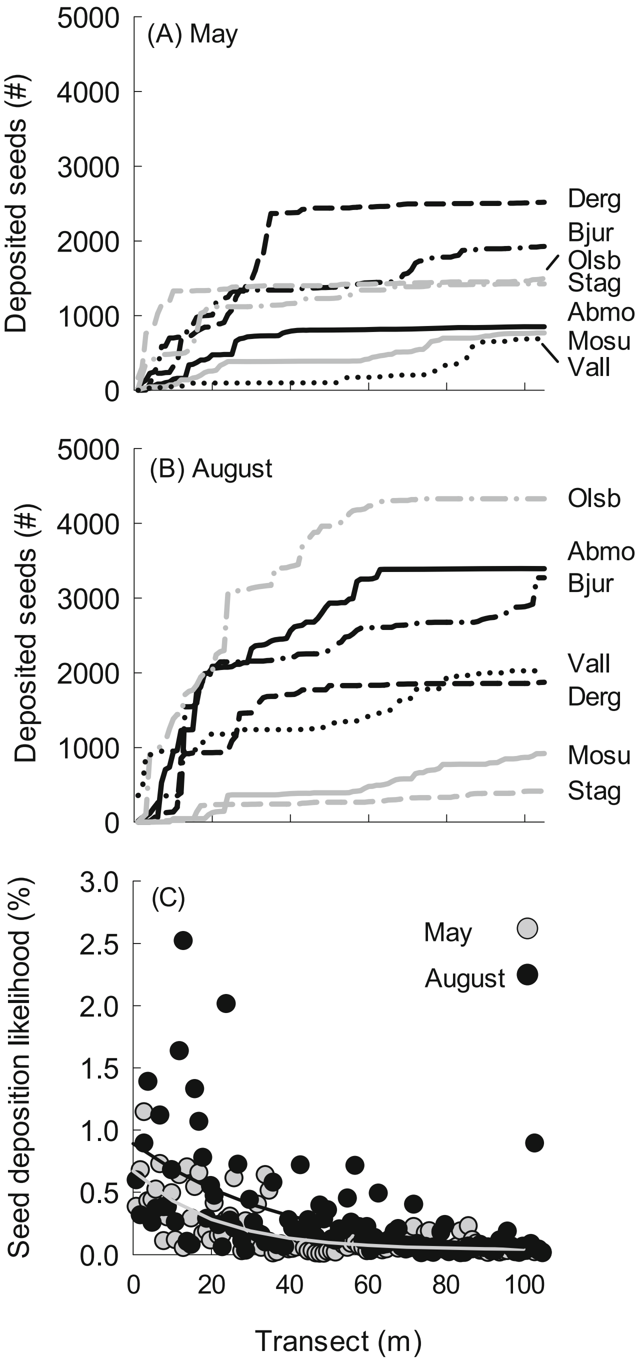

Figure 2. Longitudinal seed deposition patterns. Cumulative patterns of seed deposition of sunflower seeds that were released at the most upstream reach end in May (A) and August (B) with different line patterns for the different reaches. For reach abbreviations, see Figure 1C). (C) The seed deposition likelihood per meter of the transect, with a dot representing the mean of seven streams.

A large proportion of the seedlings were two fern species (*Gymnocarpium dryopteris* and *Phegopteris connectilis*), contributing to over 90% of seedlings in many plots (Table S2). To prevent dispersal patterns of those two fern species obscuring general patterns across other species, we excluded those fern species from our

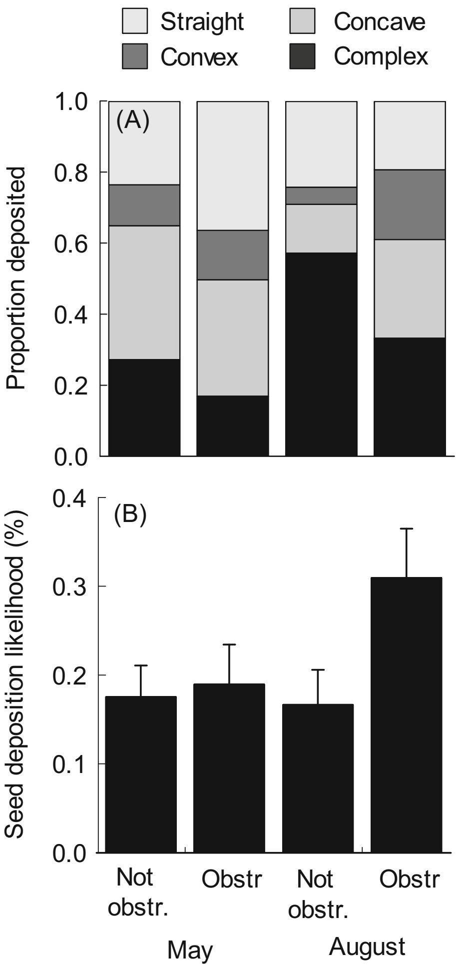

Figure 3. Bank characteristics of seed deposition patterns. Characterization of seed deposition at 1-m sections of bank with different characteristics. (A) Distribution of the deposited seeds over different bank forms, with and without obstruction. Fractions indicate the proportion of seeds and are hence standardized for the availability of the bank forms. (B) Mean seed deposition likelihood for bank sections where the flow was not obstructed or obstructed in front of a bank (e.g. by plant material or boulders within 1 m from the bank). Error bars are SE.

analysis. Without those two species, on average 11.2 ± 2.2 SE ($3802/m^2$) seeds germinated per seed bank sample, and there was no significant difference in total seedling number (linear regression; $F_{[2,56]} = 0.987$, $p = 0.379$) between the different seed deposition categories. The species number and Shannon diversity index were significantly lower for seed bank samples than in the riparian vegetation (linear regression; $F_{[1,118]} = 214.2$, $p < 0.001$ and $F_{[1,118]} = 139.7$, $p < 0.001$, respectively). Whereas the number of species did not differ significantly between seed deposition categories ($F_{[2,118]} = 1.045$, $p = 0.355$), the plots with low sunflower seed deposition (LD plots, low elevation) had lower Shannon diversity compared to both high sunflower deposition (HD plots, low elevation) and UP plots that only receive seeds via hydrochory during extreme floods. However, this relationship was not statistically significant (Fig. 4; $F_{[2,118]} = 2.818$, $p = 0.064$). Differences between deposition categories in species richness and Shannon index were similar for the seed bank and the standing riparian vegetation, as the interaction was not significant ($F_{[2,118]} = 0.247$, $p = 0.781$ and $F_{[2,118]} = 1.311$, $p = 0.273$, for species richness and Shannon index, respectively). Results including *G. dryopteris* and *P. connectilis* are given in Tables S7–S9.

Plot-Scale Relations Between Seed Bank and Vegetation Communities

We found a different species composition in the standing riparian vegetation compared to the seed bank (Fig. 5A), although some species occurred in both. In seed bank samples, *Carex nigra* (L.) Reichard, *C. vaginata* Tausch, *Potentilla erecta*, and *Betula* sp. were frequently found. The standing vegetation of the plots where the soil seed bank was sampled was dominated by grasses like *Molinia caerulea* and *Melica nutans* (L.) as well as forbs like *P. erecta*, *Lysimachia europaea* L. U. Manns & Anderb., and several *Vaccinium* shrubs. Although there appeared to be a trend in which the seed bank species composition of the UP plots was different from those of LD plots, the evidence for this was inconclusive (PERMANOVA: $F_{[2,64]} = 1.09$, $p = 0.117$; Fig. 5B). We observed that several abundant species in seed banks of UP plots were lacking in LD plots (*Caluna vulgaris*, *Deschampsia cespitosa* (L.) P. Beauv., and *C. canescens* L.). In addition, *C. nigra* and *Juncus alpinoarticulatus* Chaix. increased in LD plots compared to UP plots. In contrast, the species composition of the standing vegetation differed significantly between the UP plots and the HD plots (PERMANOVA: $F_{[2,64]} = 1.68$, $p = 0.027$; Fig. 5C). This difference was driven by the disappearance of *Rhododendron tomentosum* Harmaja, *Equisetum arvense* L., *Orthilia secunda* L., and *Empetrum nigrum* L. in HD plots. In addition, *Carex rostrata*, *Sorbus aucuparia*, *Thalictrum alpinum*, *Salix* species, and *Galium palustre* L. increased compared to UP plots. The patterns in seed bank species composition correlated to variables representing hydrochory during the spring flood in May (Fig. 5B), that is, the total number of sunflower seeds deposited on 3 m surrounding the sampled plot and in the 25 m reach section of the plot (correlation coefficient = 0.64 and 0.86 with $p = 0.036$ and 0.013, respectively). For the riparian vegetation, however, the number of boulders and other obstacles protruding from the water could not be conclusively related to community composition (Fig. 5C; correlation coefficient = 0.97, $p = 0.08$). The stress associated with the three NMDS analyses was 0.171 when including both seed bank and vegetation composition, 0.150 for seed bank composition only, and 0.182 for the vegetation composition only (Fig. 5).

Reach-Wide Correlations Between Dispersal and Seed Banks

Running explorative correlations revealed the total number of sunflower seeds deposited per 100 m reach in May correlated positively to the dissimilarity between seed bank and riparian vegetation composition (Pearson's $r = 0.768$, $p = 0.035$). This indicated that locations with higher deposition of sunflower seeds in May had a larger discrepancy between species in the

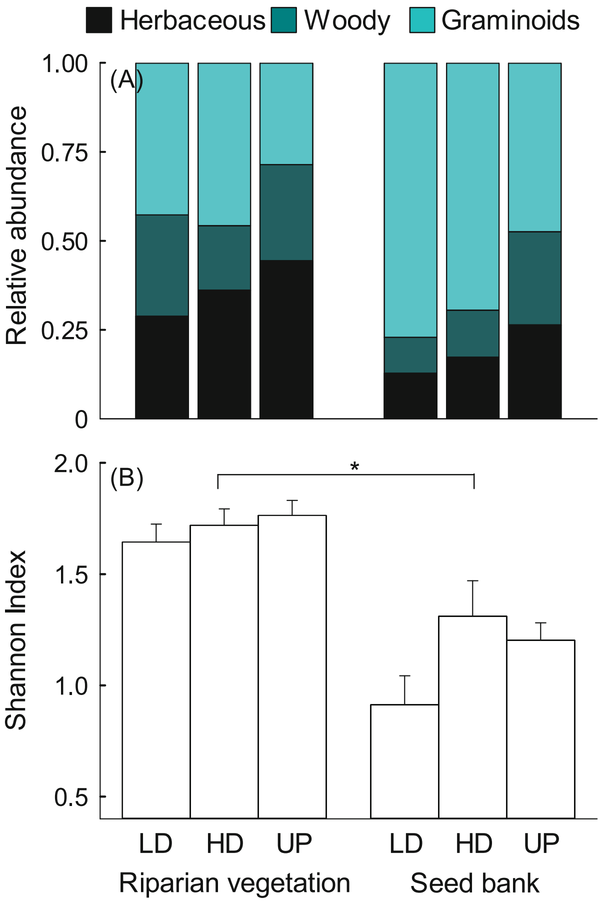

Figure 4. Differences between seed deposition categories. Distribution of (A) different species groups and (B) Shannon diversity index of the standing vegetation and seed bank at plots with, located at the water line, low (LD) and high (HD) seed deposition determined as below or above average sunflower seed deposition per meter, respectively, and for upland plots (UP). In (B), significant differences between riparian vegetation and seed bank are indicated with an asterisk. Error bars indicate SE.

seed bank and in the vegetation. The same trend was found for August, though not significant (Table S10). Reaches where more seeds were deposited in August had more homogenous vegetation (Pearson's $r = -0.768$, $p = 0.044$; Table S10). The dissimilarity between seed bank and vegetation further correlated negatively to the summed number of seeds in the seed banks of one reach (Pearson's $r = -0.893$, $p = 0.007$; Table S10), indicating that seed banks and vegetation were less alike in plots with small seed banks. With increasing time after restoration, the number of seeds in the seed bank increased, and there was a trend toward a lower vegetation dissimilarity (thus greater homogeneity) among the 12 riparian plots within one reach, although this trend was not conclusive (Table S10; Pearson's $r = -0.714$, $p = 0.072$). In addition, the channelized and newly restored reaches had a higher abundance of the two excluded fern species, and when including those two species, time since restoration correlated negatively to the total number of fern individuals per seed bank sample (Pearson's $r = -0.826$, $p = 0.022$; Table S10).

Discussion

Our study is one of the first to explicitly test the role of seed banks as the reason for a lack of restoration success of riparian zones in boreal stream systems. In these hydrogeomorphically restored systems that include no seeding or planting, we examined relationships among and between the various steps that contribute to the restoration success of riparian vegetation communities, namely, seed deposition patterns (and likelihood of seed bank formation), seed bank composition, and existing riparian plant communities. In our sunflower seed release experiment, we observed that high flow conditions, such as those associated with channelization or spring flood, decrease the sunflower seed deposition. Furthermore, we found that flow obstruction in the bank vicinity increased seed deposition and affected riparian vegetation species composition, but not seed bank species composition. Seed banks were, in general, species poor, and their species composition was related to our estimate of seed deposition via hydrochory during the spring flood. Hence, boreal stream restoration activities that result in more frequent flow obstruction and decrease flow velocity (Polvi et al. 2014) may affect seed dispersal, seed bank composition (to some extent), and finally riparian vegetation composition.

Hydrogeomorphic Complexity Restoration Affects Seed Deposition

Our results of the sunflower seed release experiment support our first hypothesis that spatial patterns of seed deposition across and within streams are related to geomorphological characteristics, especially to local obstruction in front of a bank and release speed, which reflects surface water flow velocity. Reach-wide boulder and dead wood densities have been shown to enhance seed retention of reaches (Engström et al. 2009), which we can now confirm at even smaller scales. Our finding that surface flow velocity is an important moderator of hydrochory is supported by other studies. Both those that directly observed increased seed deposition in slow flowing sections compared to rapids (Andersson et al. 2000; Engström et al. 2009; Su et al. 2019), as well as studies that found negative correlations between flow velocity and dispersal distance (Soomers et al. 2011; Sarneel et al. 2014; de Jager et al. 2019), which implies shorter distances for most seeds and likely more deposition at low flows.

While seed deposition was more likely during low flows in August, we speculate that it may be less critical for seed bank or vegetation development, even though boreal streams may carry the most seeds in autumn, which begins in August in this system (Andersson & Nilsson 2002). Seeds deposited in August could have a lower establishment success because of the restricted growing season remaining within which seeds could successfully establish (Sarneel et al. 2016) or because the seed viability is limited.

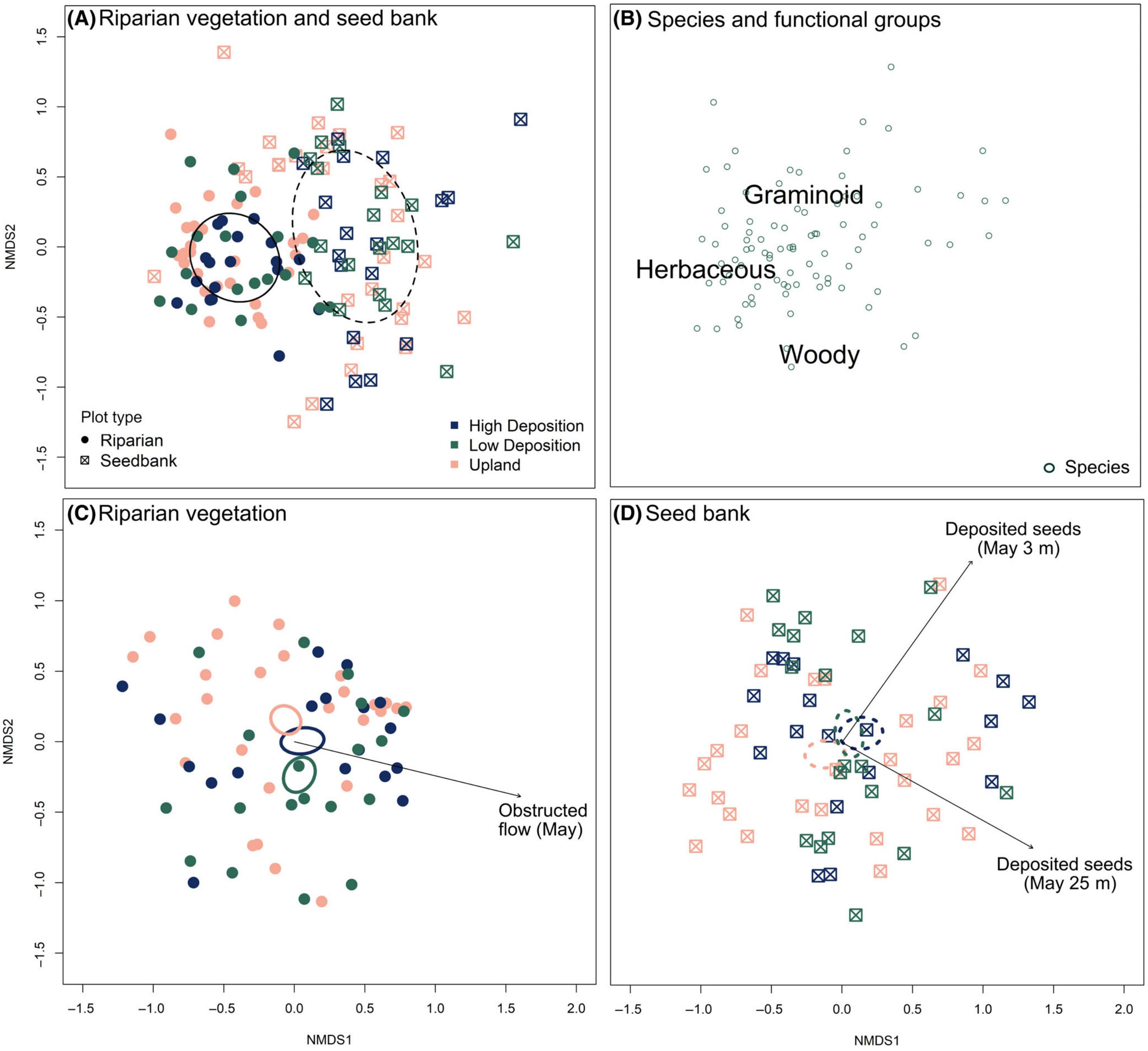

Figure 5. Species composition in riparian vegetation and seed banks. Axes 1 and 2 of the NMDS ordinations for the community composition compare (A) the different plots of the riparian vegetation and the seed bank, with one dot representing one plot, and (B) the species, including the relative abundance of woody, herbaceous, and graminoid species. In (B), one dot represents one species, and the direction and the magnitude of change in main functional species groups are indicated by the location of the words. Additional NMDS were performed to compare plots with different seed deposition categories (indicated by color) in the (C) riparian vegetation and (D) the seed bank community composition. Analyses were based on Bray–Curtis dissimilarity index on relative abundance data. Color coding reflects the plot type within a reach in all plots except (B). In panel (A), the solid and the dashed circles show the standard deviation of the weighted centroids for vegetation and seed bank, respectively. In panels (C) and (D), circles indicate the standard error around the weighted centroid. Arrows in (C) and (D) show strength and direction of significant correlations of environmental variables with the ordination space ($p < 0.1$). explanation of the environmental variables: “Deposited seeds” is the number of sunflower seeds deposited in the seed release experiment, either summed per 3 m section centered on the plot or for the 25 m section in which the plot was located. “Obstructed flow” indicates if the flow was obstructed in front of a bank or not, e.g. by protruding boulders or large debris, and the month of the measurement. Stress of the NMDS with seed bank and vegetation combined (A, B): 0.171, stress NMDS of the riparian vegetation (C): 0.182. Stress NMDS of the seed bank composition (D): 0.150.

In addition, water levels typically rise after August during autumn storms, increasing the risk of seedlings being washed from the shore (Herberg & Sarneel 2017). This may explain why “obstruction in May” and “seed deposition in May” rather than “in August” appeared as factors determining seed bank and riparian vegetation composition in our NMDS analysis.

Linking Hydrochory to the Seed Bank

In our study, the riparian seed banks contained relatively few seeds and species compared to other seed banks in Europe (Bossuyt & Honnay 2008; Kiss et al. 2018). The review by Bossuyt and Honnay (2008) found an average seed density of 13,508 seeds/m^2 across 102 published studies, which is four times larger than our mean seed density. In colder climates such as ours, many species spread clonally, which may decrease seed banks in these ecosystems (Jolivet et al. 2022). Further, frost damage may decrease seed survival in water-exposed soils in boreal riparian zones (Jaganathan et al. 2020). An additional cause for the low seed number may be that we recaptured a relatively low proportion of the sunflower seeds we released. This may suggest that only a small proportion of the high number of seeds reported to float in boreal and temperate rivers (Andersson & Nilsson 2002; Boedeltje et al. 2004) may be deposited on the bank, which would imply a low potential contribution to seed bank formation. Yet others observed that species in the seed bank have seeds with longer floating times compared to species in the vegetation (Hoppenreijs et al. 2024), which also points toward a low deposition likelihood of naturally occurring seeds.

The seed deposition likelihood, as quantified in our seed release experiment, did not appear to be a direct driver for seed density or species number in the seed bank, as these did not differ between our plots with contrasting seed deposition categories (at waterline with either low or high seed deposition and upland). Instead, we found indirect support for our second hypothesis that hydrochory contributes to seed bank formation. First, the plots situated along bank sections where seeds were less likely to be deposited tended to have a somewhat lower Shannon index, and second, our NMDS analysis suggested that the seed bank species composition was related to seed deposition in May. Despite this, the seed banks of different seed deposition categories did not differ significantly in species composition (in the NMDS). Chen et al. (2019) quantified that hydrochory contributes on average 20.4% of the total number of seed bank seeds in the three Gorges reservoirs. While this is a considerable proportion, the results of Chen et al. (2019) and those of our own in free-flowing streams suggest that seed deposition from hydrochory is not the dominant determinant of seed bank formation. Other factors that have been found to affect riparian seed banks are local dispersal (Merritt et al. 2010), stochastic disturbance, seed predation (Navarro-Ramos et al. 2022), erosion, sedimentation (O′ Hare et al. 2012), and animal activity (Wandrag et al. 2015).

Low Similarity Between Seed Banks and Riparian Vegetation

We hypothesized that if seed banks are to play an important role for vegetation development after restoration, seed bank and existing riparian vegetation composition should have been relatively similar, especially directly after restoration. Instead, we observed almost no overlap in the composition of species in the seed bank and the vegetation in our NMDS. As our riparian zones are placed within a forested landscape, the low similarity is in line with an earlier review that showed that forested systems have the least overlap between seed bank and standing vegetation compared to other ecosystems (Bossuyt & Honnay 2008). Specifically, we attribute the large discrepancy between the vegetation and the seed bank composition mostly to the absence of species in the seed bank. We did observe that the standing vegetation of the plots with high sunflower seed deposition differed from those with LD and UP plots. Because we used a balanced design and compared HD and UP plots within each reach, we believe that differences between streams in naturally floating seeds are unlikely to contribute to this difference. Hence, the relation between seed deposition and riparian vegetation may be associated with the flow regime or direct establishment from deposited seeds rather than the seed bank, as we did not observe significant differences between our seed deposition plot categories. For instance, flow regime can affect seedling survival as higher disturbance from waves, often associated with high flows, has been shown to decrease establishment by washing tiny seedlings from the shore (Sarneel & Soons 2012; Herberg & Sarneel 2017). In addition, our observation that the riparian vegetation composition was related to local flow obstruction in the NMDS may point toward the importance of disturbance from waves for establishment and vegetation composition.

In our explorative correlation analysis at reach scale, we observed the highest similarity between the vegetation and the seed banks in reaches where few sunflower seeds were deposited as well as in reaches where seed banks contained a relatively high number of seeds. Across similar spatial scales along lakes, Grelsson and Nilsson (1991) observed that seed banks and vegetation in lakeshores became less similar with decreasing wave disturbance. Since decreased wave disturbance in lakes implies slow flowing water, which we found to increase seed deposition, this aligns with our findings. These patterns may be the direct influence of hydrochory on seed bank composition, or indicate that some species are filtered out during germination from the seed bank by wave exposure and factors associated with that, such as soil organic content (Grelsson & Nilsson 1991; Sarneel & Soons 2012). Merritt et al. (2010) tried to separate the importance of wind versus water dispersal for bare soils in riparian zones. Although they found that colonization of bare soil was driven by hydrochory, the standing vegetation present at the plots resembled the species that arrived via wind. Although we did not measure deposition of natural seeds, our proxy for local/wind dispersal ("number of flower heads per plot") did not relate to existing riparian vegetation or the seed bank.

Seed Banks and Vegetation Development After Restoration

Beyond an increased understanding of factors that shape seed banks in boreal riparian zones, we aimed to evaluate the role of riparian seed banks after restoration of hydrogeomorphic complexity. This restoration often has the very general and unspecified aim to improve general environmental conditions that allow for the development of more biodiverse systems (Swedish Environmental Protection Agency home page; www.naturvardsverket.se; assessed September 2024). Given the poor seed bank we observed, the importance of seed banks for the return of species after restoration may be questionable. For a temperate lowland stream, Gurnell et al. (2006) observed that the vegetation in a newly restored river section resembled the composition of newly deposited seeds more closely than the seed bank composition, and only three species of the vegetation were solely found in the seed bank and not among seeds dispersed by wind or water. This suggests that seed banks may not contribute much to riparian restoration. However, this contrasts with the conclusions of a review by Kiss et al. (2018), who state that ecosystems adapted to frequent disturbance (such as flooding and fire) harbor the largest and most diverse seed banks, and hence, seed banks play a key role for wetland vegetation like riparian zones. More studies are needed to test when and where riparian seed banks contribute to restoration, especially in boreal systems. However, instead of a focus on the seed bank, enhancing active dispersal may be more important for boreal riparian restoration, for example by connecting nearby source populations, decreasing flow velocity, or fine-scale planning of surface water flow patterns by boulder placement closer to streambanks.

We did not find support for our hypothesized decreasing similarity between the seed bank and the vegetation with time after restoration. Instead, we found a negative correlation between the time since restoration and the total number of individuals in the seed bank. This correlation was driven by two abundant fern species and was absent when those two fern species were excluded. We believe that the decrease in abundance of the ferns *Phegopteris connectilis* and *Gymnocarpium dryopteris* with time after restoration could be related to the fact that many restoration activities aim to widen streams and hence increase light availability in the riparian zone. As indicated by a low Ellenberg value for light, these ferns prefer shade. It is therefore unlikely that their spores will germinate and affect post-restoration vegetation development. Indeed, ferns were never dominant in the standing riparian vegetation, and their abundance was barely higher in the channelized and newly restored reaches compared to reaches with a longer time since restoration.

Although our reaches spanned up to 22 years after restoration, there are indications that longer timespans may be needed for vegetation recovery as forb diversity marginally increased greater than 15 years after restoration (Hasselquist et al. 2015; Sarneel et al. 2019). However, if seed banks contribute to restoration development, they are likely to do so in bare soils shortly after restoration, as seed dispersal by other means may not have occurred. There may also be a limited role for seed banks when source populations are absent, as our results suggest that active dispersal from those populations via hydrochory may have a larger effect on vegetation development. However, in general, we conclude that riparian seed banks are unlikely to contribute to boreal riparian restoration at a local scale and could indeed be a factor that limits restoration success. However, on a larger landscape scale, boreal seed banks have the potential to increase diversity, as we found (riparian) species that solely occurred in the seed bank, and the variation within the seed bank community composition was much larger compared to the variation observed in the vegetation.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Modeled discharge in 2017.
Table S1. Characteristics of the spring flood in the study reaches.
Table S2. Relative abundance *Gymnocarpium dryopteris* and *Phegopteris connectilis*.
Table S3. Test results of effects of release velocity and month on total number of seeds stranding in each 25-m sections.
Table S4. Test results of effects of distance from the release point and month on percentage of seeds stranding in 1 m.
Table S5. Test results of bank form, the presence of flow obstruction and month on percentage of seeds stranding in 1 m.
Table S6. Results of the post hoc comparisons testing if the interaction between flow obstruction and month on the percentage of seeds stranding in 1 m of the transect.
Table S7. Outcomes of the linear models analyzing the effect of deposition plot category.
Table S8. Means and standard deviations (SD) of the species richness and Shannon index.
Table S9. Post hoc test of the contrast between the different deposition categories.
Table S10. Pearson correlations between reach characteristics, seed dispersal, year since restoration and seed bank and vegetation diversity.

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