

Functional responses of aquatic and riparian vegetation to hydrogeomorphic restoration of channelized lowland streams and their valleys

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Abstract

1. Streams and riparian zones are highly heterogeneous ecosystems. Their high biodiversity is promoted by variable flow velocities and water depths, strong hydrological gradients and disturbance regimes. However, human interventions like damming and channelization have degraded these ecosystems world-wide. And, although restoration efforts have increased in the past decades, ecological improvement is lagging.
2. We assessed vegetation development in channelized lowland stream valleys in the Netherlands, combining innovative restoration measures to the stream and stream valleys. This “stream valley restoration” entailed construction of narrower and shallower channels to increase flow velocities during base discharges, meandering of the watercourse to increase flow and depth heterogeneity and excavation of banks to create wide v-shaped stream valleys. We evaluated the effects on functional aspects of the developing in-stream and riparian vegetation by comparing restored stream reaches to nearby unrestored reaches.
3. The reduced channel dimensions led to higher flow velocities, which, through interaction with meandering, triggered a higher variability in flow and depth. Combined with enlargement of the floodplain, this promoted flooding in stream valleys and created wider environmental gradients. Plant diversity strongly increased in the floodplain area, the land–water interface and the shallow water habitat at the channel margins, but decreased in the central parts of stream channels. There, higher flow velocities led to more typically lotic (running water) in-stream plant communities, indicated by a sharp decrease in floating-leaved species and an increase in trailing species. Riparian vegetation showed a higher beta-diversity across the wider valley slopes of restored reaches, with more wetland species in areas with water-tables between 0.0 and –0.6 m, and more upland species as well.
4. *Synthesis and applications.* This study demonstrates that the combination of strongly reduced channel dimensions, remeandering and widening of riparian zones, is effective in restoring in-stream and riparian habitat heterogeneity. The restoration efforts lead to distinct immediate increases in total and beta-diversity of many typical stream and riparian plant species. Overall, this stresses the

importance of applying restoration measures to both streams and stream valleys simultaneously, considering them as a single landscape unit.

KEYWORDS

beta-diversity, flow biotopes, hydrological gradients, macrophytes, plant diversity, riparian zone, stream valleys, wetland restoration

1 | INTRODUCTION

Streams and their riparian zones are among the most diverse freshwater ecosystems world-wide (Naiman & Décamps, 1997). This diversity is generated by a high habitat heterogeneity, segregating species along gradients of water flow, water depth and substrate type in the aquatic zone (Bornette & Pujalon, 2011; Madsen, Chambers, James, Koch, & Westlake, 2001) and along the hydrological gradient in the riparian zone (Fraaije, ter Braak, Verduyn, Breeman, et al., 2015; Naiman & Décamps, 1997; Silvertown, Araya, & Gowing, 2015). Diversity of stream and riparian vegetation is further promoted by natural disturbances caused by water flow and flooding, which limit local competitive exclusion through uprooting, burial, or oxygen deprivation of established individuals and generate space for immigrant individuals that arrive in large numbers via hydrochory (Fraaije et al., 2017; Nilsson, Brown, Jansson, & Merritt, 2010). Unfortunately, these species coexistence mechanisms have been disrupted along streams across the world, due to human interventions like channelization, bank fixation, damming and water-table regulation (Malmqvist & Rundle, 2002). In the Netherlands, the vast majority of streams, typified as lowland streams by their gentle slope (0‰–5‰), low flow velocities (0.05–0.6 m/s) and tight connection between precipitation and discharge (Verdonschot & Nijboer, 2002) have been channelized in the past to support agricultural land use. Stream channels were deliberately widened and deepened during channelization, while stream valleys were narrowed and steepened. Just like in many agricultural headwater streams across the world, this led to steep trapezoidal shapes of stream channels and riparian zones. As a result, stream valley environmental heterogeneity strongly decreased and flow velocities and flooding were strongly reduced. Altogether this has reduced the presence of lotic (running water) biota in the stream, and has diminished seed arrival, establishment and persistence of wetland species in the riparian zone, leading to a decreased diversity (Baatrup-Pedersen, Friberg, Larsen, & Riis, 2005; Brooker, 1985).

Awareness of the declining biodiversity has triggered stream restoration in the past decades, often restoring hydrogeomorphic features (Jähnig et al., 2010). However, ecological improvement was lower than aimed for in many of these projects. Landscape-scale issues, like pollution and lack of nearby source populations often impeded (short-term) ecological recovery (Brederveld, Jähnig, Lorenz, Brunzel, & Soons, 2011; Jähnig et al., 2010; Rohde, Schütz, Kienast, & Englmaier, 2005). Other causes included too specific restoration goals like restoring floodplains, matching pre-degradation channel

planforms or targeting specific organism groups, without focusing on restoring river processes (Bernhardt & Palmer, 2011; Nilsson et al., 2015; Verdonschot & Nijboer, 2002). Therefore, more innovative restoration projects have been carried out in channelized lowland streams recently, targeting the entire stream valley by combining (a) a reduction in the channel dimension (channel narrowing and bed raising) to increase stream flow velocities and overbank flow, (b) remeandering to increase habitat heterogeneity and (c) excavation of banks to restore a wide, v-shaped stream valley with wider and more gradually sloping riparian zones. The objective was to re-establish a more natural range of stream flow velocities (0.1–0.8 m/s), flooding disturbances (10–200 days inundation/year) and environmental gradients (Eekhout, Hoitink, de Brouwer, & Verdonschot, 2015). It is important to evaluate the ecological success of this innovative restoration design, particularly for aquatic and riparian vegetation which provide important ecosystem functions such as food, structure, habitat diversity, stream water temperature moderation and buffering of nutrient and pollutant fluxes towards the stream (Naiman & Décamps, 1997). Previously reported success factors for restoration of in-stream vegetation include more diverse patterns of flow and depth (Haase, Hering, Jähnig, Lorenz, & Sundermann, 2013; Lorenz, Korte, Sundermann, Januschke, & Haase, 2012; Lüderitz, Speierl, Langheinrich, Völkl, & Gersberg, 2011), and, particularly for channelized lowland streams, increases in shallow areas (Lorenz et al., 2012; Pedersen, Andersen, Nielsen, & Linnemann, 2007; Pedersen, Baatrup-Pedersen, & Madsen, 2006). For riparian vegetation, diversity increases were often attributed to increased flooding (Baatrup-Pedersen, Riis, Hansen, & Friberg, 2000; Clarke & Wharton, 2000; Helfield, Capon, Nilsson, Jansson, & Palm, 2007), or to restored flow dynamics creating new mud, sand or gravel banks that are open for colonization by emergent pioneers (Hering et al., 2015; Jähnig, Brunzel, Gacek, Lorenz, & Hering, 2009; Januschke, Brunzel, Haase, & Hering, 2011; Rohde et al., 2005). Information on macrophyte responses to restoring flow velocities in channelized lowland streams is, however, limited (Pedersen et al., 2006). Moreover, riparian zone widening has mainly been investigated in the light of other ecosystem services like nutrient and pesticide removal (Smiley, King, & Fausey, 2011). We currently have very little information on the ecological quality of riparian vegetation in widened riparian zones, or on functional responses of riparian plant species to widening.

Here, we quantify the responses of both the in-stream and the riparian vegetation to innovative stream valley restoration measures that were applied to enhance the ecological quality of channelized lowland streams, targeting fish, macroinvertebrates and plants. We

did this for five streams in the Netherlands by surveying hydrogeomorphology and vegetation along the complete gradient from the channel to the upland. Specifically, we evaluated which species can be expected in the first years after restoration, focusing on life-history traits, dispersal traits and habitat preferences. Secondly, we evaluated how this translates into effects on plant diversity. We hypothesized that the higher in-stream flow velocities result in increased spatial heterogeneity and would promote more rheophilic (associated to flowing water habitat) plant species and emergent macrophytes, and thereby total in-stream plant diversity. We also hypothesized that the wider and more spatially heterogeneous riparian zones would allow utilization of more hydrological niches and thereby promote a range of wetland species, thereby enhancing both total and beta-diversity of riparian zones.

2 | MATERIALS AND METHODS

We compared aquatic and riparian habitats of innovatively restored reaches with nearby unrestored reaches of channelized lowland streams in the Netherlands, by assessing several physicochemical variables and responses of the aquatic and riparian vegetation along stream valley transversal profiles (cross-sections).

2.1 | Study sites

We studied five channelized lowland streams, of which 0.8–2 km long stream reaches were restored between 2009 and 2011. These streams included the Hagmolenbeek (HM; 52°13′0.3″N, 6°43′16.9″E), Hooge Raam (HR; 51°42′57.7″N, 5°42′9.3″E), Kleine Aa (KA; 51°35′39.9″N, 5°16′38.7″E), Luntersche beek (LB; 52°4′46.4″N, 5°32′37.2″E) and Tengelroyse beek (TR; 51°14′42.7″N, 5°53′12.7″E), all restored in 2011 except HM (2010) and the channel at HR (2009). Average annual discharges of the streams amounted to 0.12, 0.15, 0.85, 0.40 and 1.09 m³/s, respectively, based on hourly data of local water boards in 2012. All study locations are characterized by sandy soils (Aeolian sand deposits) with catchments dominated by agricultural land use. The streams flow mainly through non-forested areas, with water-tables regulated by weirs, and yearly mowing applied to the aquatic and predominantly herbaceous riparian vegetation. Restoration involved innovative measures that affected the entire stream valley: removal of weirs and reduction in channel dimension (channel narrowing and bed raising) to increase stream flow velocities and overbank flow, remeandering to increase habitat heterogeneity (not at HR) and excavation of banks to restore a widened, v-shaped stream valley at all streams. At each study location we selected a restored reach and nearby unrestored, still channelized, reach (distances between them 0.3–1.2 km). Unrestored reaches were located upstream of restored reaches at HR and KA, and downstream at HM, LB and TR. During restoration, all pre-existing vegetation was removed. At HM only, the newly created riparian zone was sown with *Lolium perenne*, *Trifolium repens* and *Phleum pratense* subsp. *pratense* (all species nomenclature following

van der Meijden, 2005) to reduce erosion immediately after restoration. No vegetation management occurred yet at the restored reaches during the study period, except at HM (yearly mowing of aquatic and riparian vegetation) and KA (yearly mowing of riparian vegetation).

2.2 | Study design

We compared several physicochemical and vegetation parameters between paired treatment (restored) and control reaches (unrestored) of each study location. In-stream parameters were assessed in detail at the study locations HM, KA and LB (not at HR and TR due to time limitation). Riparian habitats were assessed at all study locations. To capture the higher habitat heterogeneity at restored reaches while keeping an acceptable sampling effort, in-stream, three representative sections were selected at the unrestored reach (all straight stretches) and six sections (three in a bend and three in straight stretches) at the restored reach. Per in-stream section five transects were laid out, at least 5 m apart and perpendicular to the stream flow. Each in-stream transect consisted of a continuous string of plots (25 × 25 cm) completely crossing the channel (Figure 1). For the riparian habitat, three replicate transects of five plots (25 × 50 cm) were laid out across the riparian zone within each reach. Riparian transects were placed perpendicularly to the stream channel at one side of the stream where land access was permitted and livestock was excluded, with 25–50 m distance between transects. The plots within a riparian transect covered the complete hydrological gradient from the channel to just above the estimated yearly inundation zone, with consecutive distances of ca. 0.5, 1.0, 3.0 and 5.0 m between them (low to high elevation) (Figure 1).

2.3 | Physicochemical variables

We mapped the stream and riparian zone transversal profiles using a GNSS-GPS Real Time Kinematic rover (Ashtech ProMark 800) in May 2013. Water-tables and surface water levels were monitored hourly in 2012 and 2013 using barometrically compensated pressure transducers (Schlumberger Water Services, Delft, the Netherlands; Keller Meettechniek B.V., Reeuwijk, the Netherlands) in 1–2 m deep piezometers at each riparian plot and in surface water level gauges within 30 m of the nearest riparian transect. Average summer water levels of the year 2013 (April–October) were used for further analyses. Riparian zone width and channel width were determined for the average summer water level situation, defined as the distance between the land–water interface and the highest riparian plot per transect, and distance between the banks respectively. Flow velocity was determined once at three to four plots per in-stream transect, evenly spaced over the central 3/5 part of the stream channel, during representative discharge conditions in May 2013. Nutrient availability and substrate characteristics were measured to help interpret vegetation responses. Soil nutrient availability (extractable N and P) was measured once on three combined soil cores (4 cm diameter, 10 cm depth) per riparian plot, and per in-stream section in

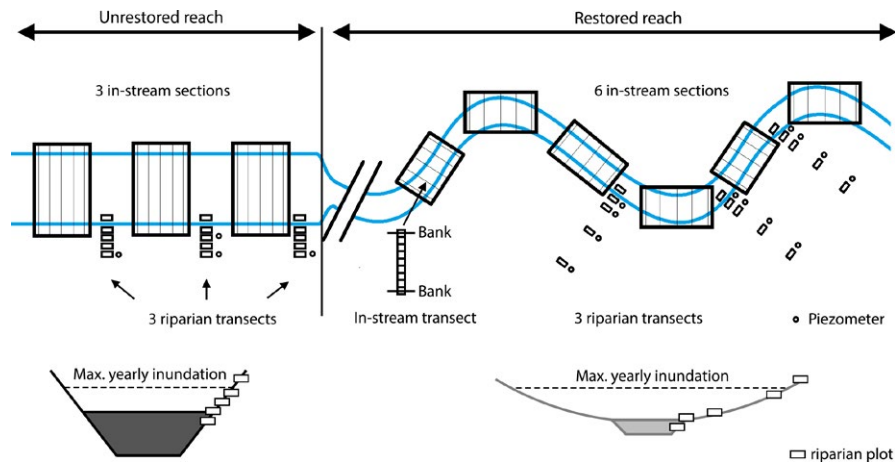


FIGURE 1 Overview of the experimental set-up in the field, with a representation of cross-sectional profiles below. At each study location, nine in-stream sections were selected, of which three in the unrestored reach, and six in the restored reach (three in straight stretches, and three in bends). In each in-stream section five cross-channel transects were laid out perpendicular to the stream flow, consisting of a continuous string of 25×25 cm plots. Riparian plots were laid out in six transects, of which three at the restored reach, and three at the unrestored reach. Each riparian transect consisted of one in-stream plot and four plots at increasing elevations along the riparian gradient, up to just above the yearly inundation zone. Piezometers were installed to monitor water levels at riparian plots

April/May 2012/2013 (details in Supporting Information Appendix S1). In-stream substrate type was recorded per in-stream plot by visual estimation of the dominant substrate in the first 10 cm of soil, distinguishing stone (>60 mm diameter), gravel (3–60 mm), sand (0.25–3 mm), silt (<0.25 mm), hard clay and peat, once in May 2013.

2.4 | Vegetation surveys and species traits

Plant species cover per plot was registered once in June (in-stream, using a viewing tube) and July/August (riparian zone) 2013, with cover of layered vegetation summed. We compiled the following plant and seed traits: plant C-S-R functional signature (i.e. coordinates in “C-S-R space” providing a numerical index for the degree of adaptation to a strategy; cf. Hunt et al., 2004), moisture preference as indicated by Ellenberg *F*-value (Ellenberg, 1988, adjusted by Hill, Mountford, Roy, & Bunce, 1999), and the dispersal traits plant life span (annual/perennial), seed buoyancy (% seeds afloat after 1 week in water), seed mass (g) and seed terminal velocity (m/s) (from the LEDA traitbase, Kleyer et al., 2008). For the in-stream vegetation we classified species using the vegetative units of vascular plant species of the functional habitat classification by Harvey, Clifford, and Gurnell (2008), grouping growth forms by their association with (a) fast flow: trailing vegetation, species rooting in the bank but trailing over the water (like *Agrostis stolonifera* or *Nasturtium officinale*); (b) intermediate fast flow: submerged fine-leaved macrophytes, submerged species with leaves at least 4 times longer than wide (*Potamogeton pectinatus* or *Ranunculus* ssp.); (c) intermediate slow flow: submerged broad-leaved and emergent macrophytes, submerged species with leaves less than four times longer than wide (*Callitriche* spp.) as well as submerged linear-leaved plants (*Sparganium emersum*), and emergent broad-leaved herbs (*Lycopus europaeus*) as well as emergent reeds (*Typha latifolia*); and (d) slow flow: floating-leaved macrophytes, floating-leaved species

(*Potamogeton natans*) as well as free-floating species (*Lemna* spp.). A complete overview of all identified species and their trait values is available in Supporting Information Appendix S2.

2.5 | Data analysis

To test if physicochemical or vegetation response variables differed between restored and unrestored reaches, we compared (generalized) linear mixed models (GLMMs) (R package LME4; Bates, Maechler, Bolker, & Walker, 2014) with and without restoration as an explanatory variable, using Kenward–Roger *F* tests (LMMs, R package lmerTest; Kuznetsova, Brockhoff, & Christensen, 2017) or chi-squared likelihood ratio tests (GLMMs) to determine significance ($p < 0.05$). Transect, section (only for in-stream) and study site (i.e. a selected stream) were included as nested random effects (intercept) for analyses on the plot scale, section nested in study site for analyses on the in-stream transect scale, and study site for analyses on the reach, in-stream section and riparian transect scales.

GLMMs were used for analyses on all non-continuous response variables, using a Poisson error distribution for species richness and a binomial error distribution for growth form occurrence, substrate type occurrence and Bray–Curtis dissimilarity of the vegetation. LMMs were used for analyses on all continuous response variables (all remaining variables), using log- or arcsine-transformation of response variables to improve normality when necessary, based on the Shapiro–Wilk test (R package stats). Community-weighted trait means of the vegetation were calculated by incidence weighting, yielding the mean trait value of all present species with available trait values.

To account for possible differential responses to restoration influenced by water level we tested the effects of the explanatory variables restoration, water level (continuous variable to capture detailed responses along the hydrological gradient) and their interaction for the response variables using the above-described

models. We tested all combinations of fixed effects and selected the best model on the basis of Akaike's information criterion (AIC). Significant model improvement by addition of a fixed effect was defined as a decrease in AIC by at least 2 units compared to the reduced model (Burnham & Anderson, 2002).

To analyse beta-diversity (species turnover) along the riparian hydrological gradient, we first calculated water level distances and Bray–Curtis dissimilarities of the plant communities between all pairs of plots within a riparian transect, using the R package VEGAN (Oksanen et al., 2015). We then corrected the observed dissimilarities for differences in alpha diversity between restored and unrestored reaches using a null-model approach as in Myers, Chase, Crandall, and Jiménez (2015). In the null model, species in a riparian transect were distributed at random, while holding the number of species within each plot constant, thus removing species distribution patterns along the riparian gradient. Compositional dissimilarities between all pairs of plots within a transect from these simulated communities (i.e. expected dissimilarities) were used to correct the observed dissimilarities. This was done by calculating a standardized effect size (beta-deviation) obtained by subtracting the mean expected dissimilarity (of 2,000 null model iterations) from the observed dissimilarities, divided by the standard deviation of the expected dissimilarities.

3 | RESULTS

3.1 | Physicochemical variables

There were clear differences in physical and chemical characteristics between the restored and unrestored reaches (Table 1; Supporting Information Appendix S3 per study location). In-stream, the restored reaches showed larger areas of shallow water habitats, higher flow velocities and higher flow and depth variability than unrestored reaches. The number of plots with silt and stones (bank reinforcement stones) as dominant substrates significantly decreased at all restored reaches, while sand substrate significantly increased. Riparian zones of restored reaches were significantly wider than at unrestored reaches with larger areas of wet riparian habitats (water tables of 0.0 to –0.3 m) and of moist zones with slightly deeper water tables (water tables of –0.3 to –0.6 m). Surface water levels showed larger fluctuations at restored reaches (although this trend was not significant), leading to an average of 75.2 days/year of overbank flow versus 0.8 day/year at unrestored reaches. Topsoil removal lowered soil N and P availability at the restored reaches in the riparian zone as well as in the stream sediment.

3.2 | Vegetation characteristics, plant life history and dispersal traits

A total of 159 species were observed in the vegetation surveys of which 122 at restored reaches and 97 at unrestored reaches. Average cover per plot was 83% (riparian plots) and 27% (in-stream plots) at restored reaches, which was clearly lower than at

unrestored reaches (115% and 52%; *SD*'s and model statistics in Table 2). All study sites were dominated by herbaceous plant species. Average cover of woody species was only 3% and 0.04% at the riparian plots of restored and unrestored reaches respectively. In the first 2 years after restoration, mainly pioneer species with high dispersal capacities colonized the restored reaches (see Supporting Information Appendix S2 for a complete list). These species had significantly higher scores for the “ruderal” strategy and lower scores for the “competitor” strategy (Table 2). Moreover, they had a shorter life span, lower seed mass and higher ability for water dispersal (seed buoyancy) than at unrestored reaches. For the riparian vegetation, seed dispersal ability by wind was also significantly higher (i.e. lower seed terminal velocity) at restored reaches (Table 2).

3.3 | In-stream vegetation

In-stream vegetation showed a slow colonization after restoration, toward only half of the coverage of unrestored reaches. Overall, diversity of the in-stream vegetation did not differ between plots at restored and unrestored reaches (Table 2). At deeper habitats, however, diversity was clearly lower at restored than at unrestored reaches, while at the shallow water habitats near the banks, diversity was comparable or higher at the restored reaches (Figure 2 upper panel; significant interaction between restoration and water depth; Supporting Information Appendix S4). Overall lower Ellenberg *F*-values at restored reaches indicate an increase in wetland or terrestrial species occurring in the stream (Table 2), which was supported by higher diversities of these species groups at shallow water habitats near the banks (Ellenberg *F*6, *F*7, *F*9; Figure 2 right panels; Supporting Information Appendix S4 for model statistics).

At restored reaches, a shift to more typically lotic in-stream vegetation communities was observed, indicated by a significantly lower occurrence and diversity of floating-leaved vegetation (associated to slow flow), and a slight increase in trailing species (associated to fast flow), although the latter was not significant due to low overall presence (Figure 3; Supporting Information Appendix S4 for model statistics). Occurrence of the other in-stream growth forms showed no overall response to restoration. Significant interactions between restoration and water depth, however, show that restoration affected these growth forms at specific water depths. At intermediate water depths, occurrence (and diversity) of the submerged fine- as well as broad-leaved growth forms was slightly higher at restored reaches than at unrestored reaches, while for emergent species this was the opposite. At the land–water interface, on the contrary, emergent species showed a much higher diversity at restored than at unrestored reaches (Figure 3; Supporting Information Appendix S4).

3.4 | Riparian vegetation

Riparian vegetation colonized quickly after restoration, reaching a significantly higher species diversity than at unrestored reaches at the reach, transect and plot scale (Table 1). The largest increase in

TABLE 1 Means \pm standard deviations of physicochemical characteristics at restored versus unrestored reaches, with the scale of measurement, and test statistics of LMMs (Kenward–Roger F tests) or GLMMs (chi-squared likelihood ratio tests). Significantly higher values between restored and unrestored reaches ($p < 0.05$) are underlined

	Restored, mean (\pm SD)	Unrestored, mean (\pm SD)	Scale	Test statistic	p
Geometry				F	
Channel width (m)	5.32 (\pm 2.22)	<u>8.22 (\pm1.51)</u>	In-stream transect	18.4	<0.001
Channel width, subsection between 0.0 and 0.3 m water depth (m)	<u>2.43 (\pm1.38)</u>	1.00 (\pm 0.27)	In-stream transect	30.1	<0.001
Riparian zone width (m)	<u>11.42 (\pm4.76)</u>	2.31 (\pm 0.38)	Riparian transect	1,100.2	<0.001
Riparian zone width, subsection with water tables 0.0 to -0.3 m (m)	<u>4.65 (\pm3.48)</u>	0.61 (\pm 0.17)	Riparian transect	117.7	<0.001
Riparian zone width, subsection with water tables -0.3 to -0.6 m (m) ^a	<u>4.98 (\pm3.65)</u>	0.75 (\pm 0.26)	Riparian transect	88.3	<0.001
Channel depth (m)	0.42 (\pm 0.35)	<u>0.78 (\pm0.38)</u>	In-stream plot	54.8	<0.001
Spatial coeff var channel depth (SD/mean)	<u>0.55 (\pm0.12)</u>	0.41 (\pm 0.08)	In-stream transect	28.6	<0.001
Hydrology				F	
Flow velocity (m/s)	<u>0.16 (\pm0.08)</u>	0.04 (\pm 0.01)	In-stream transect	69.3	<0.001
Overbank flow (# days in 2012)	<u>75.2 (\pm49.8)</u>	0.8 (\pm 1.8)	Reach	29.2	0.006
Spatial coeff var flow velocity (SD/mean)	<u>0.41 (\pm0.27)</u>	0.30 (\pm 0.18)	In-stream transect	4.4	0.048
Temp coeff var surf wl (SD/mean E-01, in 2012)	0.17 (\pm 0.13)	0.14 (\pm 0.08)	Reach	3.2	0.147
Nutrient availability (mg/kg dry soil)				F	
N-avail stream sediment	4.98 (\pm 3.73)	<u>5.98 (\pm2.21)</u>	In-stream section	12.2	<0.001
P-avail stream sediment	5.72 (\pm 3.78)	<u>8.54 (\pm2.71)</u>	In-stream section	32.5	<0.001
N-avail riparian soil	2.27 (\pm 3.92)	<u>6.49 (\pm3.72)</u>	Riparian plot	73.2	<0.001
P-avail riparian soil	4.78 (\pm 5.88)	<u>10.90 (\pm9.69)</u>	Riparian plot	18.9	<0.001
In-stream substrate (% of plots in which a substrate type dominated)				χ^2	
Gravel	0.4 (\pm 6.4)	1.7 (\pm 12.9)	In-stream plot	0.0	0.826
Clay	7.1 (\pm 25.7)	0 (\pm 0)	In-stream plot	0.3	0.578
Peat	6.4 (\pm 24.5)	0 (\pm 0)	In-stream plot	0.2	0.620
Sand	<u>85.3 (\pm35.4)</u>	44.3 (\pm 49.7)	In-stream plot	13.3	<0.001
Silt	0.8 (\pm 8.7)	<u>45.8 (\pm49.8)</u>	In-stream plot	20.2	<0.001
Stones	0 (\pm 0)	<u>8.2 (\pm27.4)</u>	In-stream plot	17.2	<0.001

Note. LMM: linear mixed models; GLMM: generalized linear mixed models.

^aOne outlier was removed from this comparison.

diversity was observed in the moist parts of the riparian zone with water tables of 0.0 to -0.6 m (Figure 2). Species associated with wet soils (Ellenberg $F7$, $F9$) strongly increased in diversity in this zone, as did species more typical for dry soils (Ellenberg $F4$, $F5$; Figure 2, model statistics in Supporting Information Appendix S4). Mean Ellenberg F -values of riparian vegetation were similar between restored and unrestored reaches, and a similar vegetation zonation was observed along the riparian gradient (Figure 2). However, the wider riparian zones of restored reaches showed a significantly higher species turnover (beta-diversity) along the hydrological gradient (Figure 4; Supporting Information Appendix S4). After correction for differences in alpha diversity (beta-deviation), this difference remained significant, though with a lower effect size (Supporting Information Appendix S4).

4 | DISCUSSION

4.1 | Hydrogeomorphic and physicochemical changes by restoration

The reaches with restored hydrogeomorphology were characterized by significantly more shallow and narrow transversal channel dimensions, and much wider, more gradually sloping, riparian zones. The reduced channel dimensions stimulated flooding in the riparian zone and led to higher flow velocities, which, through interaction with meandering and vegetation patches, invoked significantly higher spatial variability in flow and depth, including the formation of bare sandbanks (Eekhout et al., 2015), at the restored reaches. Moreover, excavation of new channels in sandy soils, topsoil removal at riparian

TABLE 2 Means \pm standard deviations of in-stream and riparian vegetation characteristics, showing species richness on different scales (the number of unique species on each scale), and plot-scale values for total plant cover and community-weighted trait means of the vegetation (Ellenberg *F*, life history and dispersability). Significantly higher values (between restored and unrestored reaches) are underlined, based on model statistics of LMMs (Kenward-Roger *F* tests) or GLMMs (Chi-square likelihood ratio tests) with $p < 0.05$. In-stream species richness could only be compared on the plot scale due to unequal number of plots between restored and unrestored reaches

	In-stream vegetation				Riparian vegetation			
	Mean rest	Mean Unr	Test statistic	<i>p</i>	Mean rest	Mean Unr	Test statistic	<i>p</i>
Species richness			χ^2				χ^2	
Reach scale					<u>42.2 (± 5.2)</u>	27 (± 5.7)	16.8	<0.001
Transect scale					<u>27.3 (± 4.1)</u>	16 (± 4.7)	45.0	<0.001
Plot scale	2.1 (± 1.7)	2.4 (± 1.4)	1.7	0.187	<u>8.6 (± 4.2)</u>	6.3 (± 2.9)	15.1	<0.001
			<i>F</i>				<i>F</i>	
Total plant cover (%)	27.0 (± 36.3)	<u>51.6 (± 46.1)</u>	11.3	0.003	82.8 (± 42.7)	<u>114.7 (± 45.8)</u>	5.4	0.028
Ellenberg <i>F</i> -value	10.57 (± 1.18)	<u>10.90 (± 0.68)</u>	11.5	0.003	7.54 (± 1.75)	7.34 (± 1.55)	0.4	0.539
Life history			<i>F</i>				<i>F</i>	
Competitors (C score)	0.45 (± 0.14)	<u>0.56 (± 0.17)</u>	15.9	<0.001	0.39 (± 0.11)	<u>0.67 (± 0.14)</u>	123.4	<0.001
Stress tolerators (S score)	0.01 (± 0.04)	<u>0.06 (± 0.08)</u>	8.8	0.007	0.11 (± 0.07)	0.10 (± 0.08)	0.8	0.373
Ruderals (R score)	<u>0.54 (± 0.14)</u>	0.38 (± 0.22)	17.5	<0.001	<u>0.50 (± 0.11)</u>	0.23 (± 0.12)	253.1	<0.001
Life span (annual=1, perennial =2)	1.73 (± 0.29)	<u>1.91 (± 0.15)</u>	11.1	0.003	1.76 (± 0.16)	<u>1.97 (± 0.08)</u>	104.8	<0.001
Dispersability			<i>F</i>				<i>F</i>	
Seed buoyancy (% floating after 1 week)	77.5 (± 23.9)	68.5 (± 23.9)	1.1	0.315	<u>76.1 (± 24.5)</u>	62.0 (± 20.2)	15.4	<0.001
Seed terminal velocity (m/s)	1.44 (± 0.6)	2.23 (± 1.26)	3	0.099	1.70 (± 0.49)	<u>2.31 (± 0.59)</u>	17.1	<0.001
Seed mass (mg)	1.17 (± 2.16)	<u>9.76 (± 12.13)</u>	23.2	<0.001	0.74 (± 0.75)	<u>2.37 (± 2.86)</u>	14.9	<0.001

Note. LMM: linear mixed models; GLMM: generalized linear mixed models.

zones and higher flow velocities flushing silt substrates (cf. Madsen et al., 2001), strongly lowered silt substrate and nutrient availability at the restored reaches. This additionally enhanced the potential for plant species coexistence in the riparian zones (Soons, Hefting, et al., 2017), and stimulated more favorable substrate conditions for, for example a diverse benthic macroinvertebrate community (Wood & Armitage, 1997).

4.2 | Responses of plant species and diversity to hydrogeomorphic restoration

Excavations during hydrogeomorphic restoration had cleared all existing vegetation. The subsequent lack of interspecific competition stimulated an often observed immediate increase in diversity compared to the unrestored situation (Noon, 1996). The increase in diversity was most pronounced in the area covering the floodplain, the land-water interface and the shallow water habitat near the banks at all streams. This indicated that the increased flooding

and flow-induced habitat heterogeneity contributed to the higher diversity at restored reaches. Previously reported mechanisms for such rises in diversity include increased hydrochorous propagule arrival in riparian zones (Fraaije, ter Braak, Verduyn, Verhoeven, & Soons, 2015; Nilsson et al., 2010), stimulated coexistence of pioneers and competitors by disturbances through flooding and sedimentation (Januschke et al., 2011; Rohde et al., 2005) and increased availability of shallow water habitat (Lorenz et al., 2012; Pedersen et al., 2006). Moreover, the more natural flooding dynamics may have enhanced effective seed dispersal to suitable micro-sites, promoting successful establishment and diversity (Soons, de Groot, et al., 2017).

Flooding-related disturbance effects, leading to windows of opportunity for colonization, may not yet have been responsible for the increased alpha diversity at our restored reaches, since many open spots in the vegetation occurred in the primary successional stage. The restored flooding regimes and flow dynamics, however, did induce a higher habitat differentiation along the

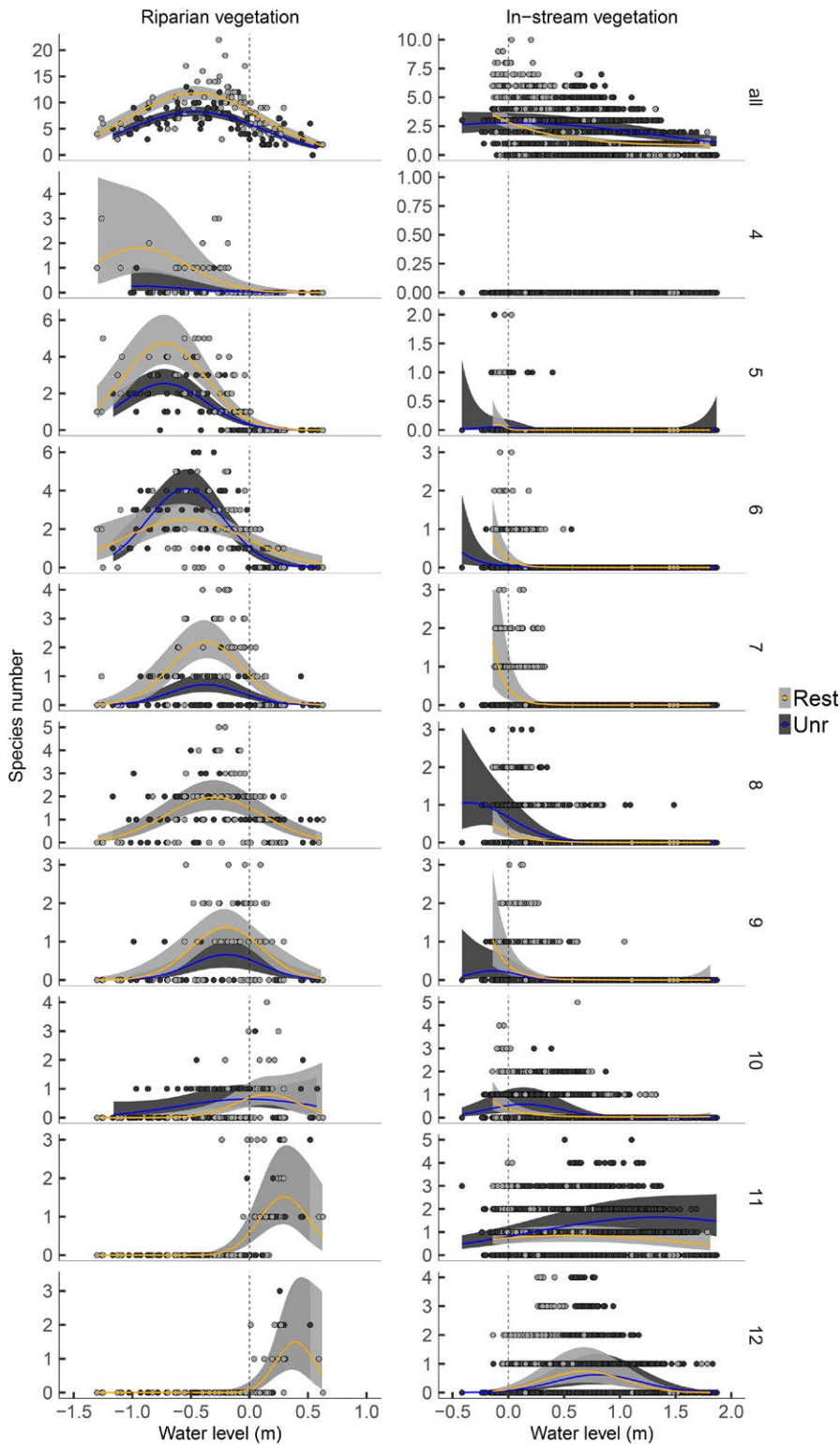


FIGURE 2 Plot-scale species richness for the riparian (left panels) and in-stream (right panels) vegetation, with the total number of species (upper panel) and the number of species per Ellenberg F-class (nine panels below) as indicated on the right of the panels. Restored and unrestored reaches are separated by colour. Negative water levels represent depths of phreatic water-tables in the riparian zones, and positive values indicate water depths in the stream channels. Continuous lines represent best model fits of generalized linear mixed models (GLMMs) to the field data (dots), with the grey ribbons indicating 95% confidence intervals (based on fixed effects only). For model statistics see Supporting Information Appendix S4

riparian slopes, which together with widening led to a significantly higher spatial species turnover (lateral structuring) of the riparian vegetation at restored reaches. Kuglerová, Botková, and Jansson (2017) reported similar results and attributed the increased turnover to the higher habitat differentiation at restored reaches. We expect that both increased space by widening and increased habitat differentiation contributed to opening up hydrological niches

(cf. Silvertown et al., 2015) in our study since hydrological niches around the land–water interface hardly existed at the steep and narrow riparian slopes of the unrestored, channelized reaches. Based on our data it is, however, not possible to judge their individual contribution to the vegetation responses, as was also the case in comparable studies (Clarke & Wharton, 2000; Hering et al., 2015).

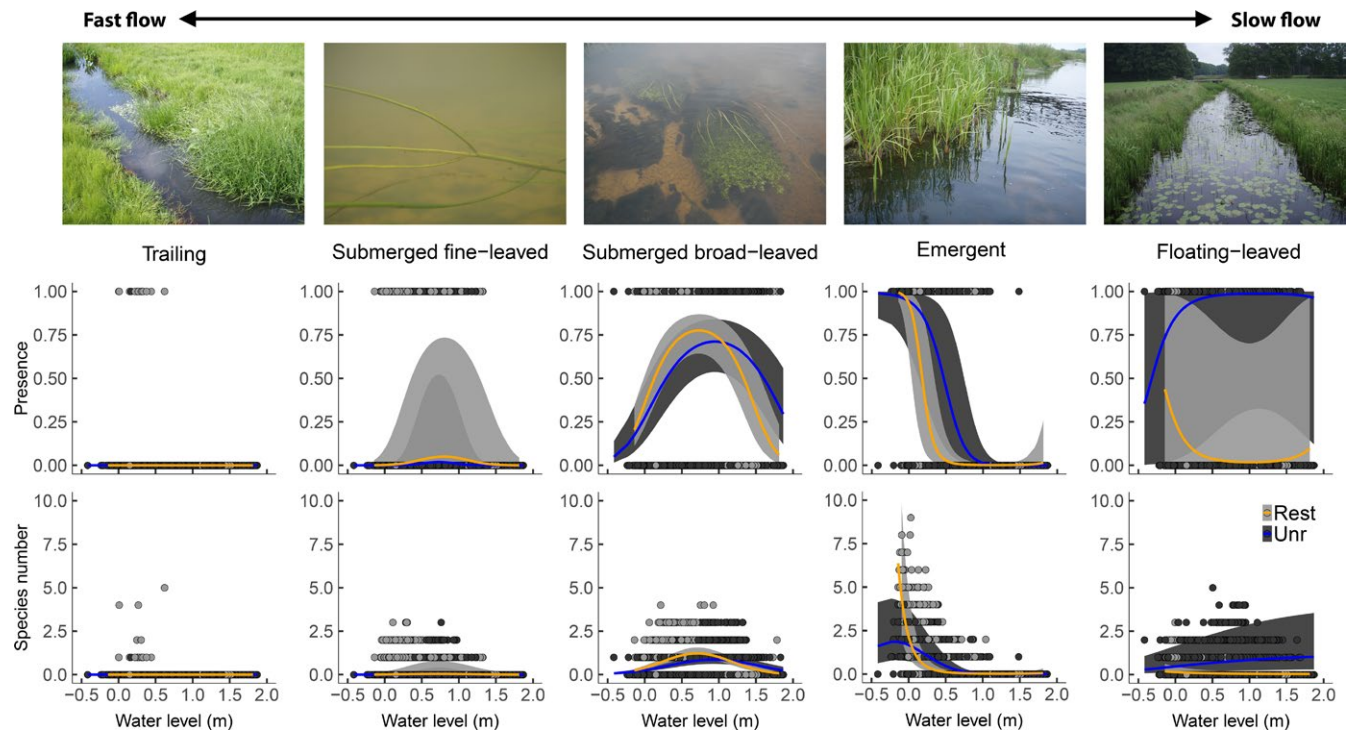


FIGURE 3 In-stream vegetation differences between restored (light grey, orange lines) and unrestored (dark grey, blue lines) reaches, showing probability of occurrence (upper five graphs) and species richness (lower five graphs) of different growth forms per in-stream plot along the water level gradient. Negative water levels represent depths of phreatic water tables in the riparian zones, and positive values indicate water depths in the stream channels. Growth forms are ordered from left to right according to their association with more lotic habitats (left) or more lentic habitats (right), with the submerged broadleaved and emergent growth forms associated to the same flow conditions. Continuous lines represent best model fits of generalized linear mixed models (GLMMs) to the field data (dots). 95% confidence intervals (based on fixed effects only) are indicated by the grey ribbon. Model statistics are available in Supporting Information Appendix S4

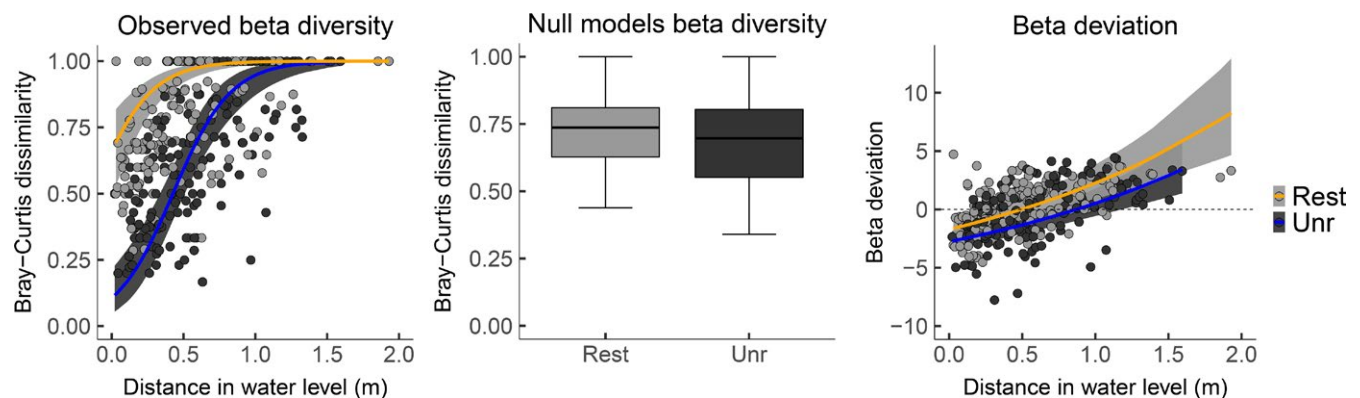


FIGURE 4 Beta-diversity along the riparian hydrological gradients expressed by Bray-Curtis dissimilarities between all pairwise combinations of plots within riparian transects, plotted against water level distance between the plot pairs, with the observed beta-diversity (left panel), beta-diversity of null models (central panel; see Methods) and standardized effect size of beta-diversity (the observed beta-diversity corrected for the null model outcomes; right panel), for the riparian zones of restored (light grey, orange lines) and unrestored (dark grey, blue lines) reaches. Continuous lines represent best model fits of generalized linear mixed models (GLMMs) to the field data (dots). 95% confidence intervals (based on fixed effects only) are indicated by the grey ribbon. For model statistics see Supporting Information Appendix S4

The higher beta diversity of the riparian vegetation at restored reaches compared to unrestored reaches remained significant, but the explained variance was relatively small after correction for differences in alpha diversity. This can be related to the primary successional stage: at restored reaches both wetland and upland species (Ellenberg F 4–10)

benefited from the widened areas of moist soils. More fierce interspecific competition may eventually displace the upland species to the drier ends of the gradients (Wisheu & Keddy, 1992), intensifying lateral structuring of the riparian vegetation. More fierce interspecific competition could, however, also oust less competitive wetland species when

succession proceeds. This would lead to a decrease in alpha diversity (Noon, 1996), and, in case species become outcompeted from the riparian gradient completely, also in beta-diversity. Disturbance dynamics by flow and flooding will remain of crucial importance to maintain the higher alpha and beta-diversity by limiting the expansion of highly competitive species (Januschke et al., 2011; Rohde et al., 2005).

In contrast to the riparian vegetation, in-stream vegetation responded to the restoration measures with a significant reduction in diversity and coverage in the central parts of the stream channels. Previous studies found similar results 2 years after restoration, and attributed the slow colonization to the predominance of unconsolidated sandy substrates unsuitable for colonization, and to limited upstream source populations (Baattrup-Pedersen et al., 2000; Biggs et al., 1998). Because relatively close source populations were present upstream of our study sites (between 150 and 800 m) and flowing stream water has been shown to cause seedling breakage or uprooting (Riis & Biggs, 2003) and lead to limited propagule retention (Riis, 2008), we think that mainly the higher flow velocities at restored reaches impeded in-stream vegetation colonization. The relatively low explained variance for this reduction in diversity and coverage was caused by large variation among transects, arising from the patchy distribution of aquatic vegetation in streams.

The successfully colonized in-stream vegetation at restored reaches differed from that of unrestored reaches by showing a sharp decrease in floating-leaved species, and slight increases of trailing and submerged fine-leaved species. This indicates that, at the restored reaches, more typically lotic in-stream plant communities developed than at unrestored reaches (cf. Harvey et al., 2008). The lower occurrence of rooted floating-leaved and emergent species in the central parts of restored stream channels may be related to the lower anchorage strength and drag-reducing capacities of these species (Bal et al., 2011). Free-floating individuals were more easily washed away at restored reaches due to the higher flow velocities, and the increase in trailing species, and of emergent species at the land-water interface was most presumably stimulated by the increase in habitat availability, as has also been found by Pedersen et al. (2006). Comparable responses of aquatic vegetation to higher flow velocities in streams and rivers have been reported previously but at relatively high flow velocities (around 0.4 m/s; Meyer, Combroux, Schmitt, & Trémolières, 2013; or 0.24 m/s; Pedersen et al., 2006). Our study indicates that mean flow velocities of 0.16 m/s were already effective in stimulating more rheophilic plant communities, at least in the first 2 years after restoration.

4.3 | Implications for future stream and stream valley restoration

Our results indicate that particularly the combination of restoration measures, where wide, gradually sloping floodplains and flooding are restored while in-stream summer flow is maintained, is essential to restore typical wetland vegetation and plant species diversity in channelized lowland streams and their valleys. This requires strong reduction in channel dimensions, which can only be applied when

sufficient space is available in the stream valley for inundation during higher discharges. These results stress the importance of applying a well-coordinated suite of restoration measures at once, focusing on the stream and its valley as a single landscape unit to restore river processes (Bernhardt & Palmer, 2011), instead of carrying out restoration measures on only specific parts of the ecosystem.

The predominance at the restored sites of ruderal species and species with adaptations to wind dispersal (low terminal velocity; Soons, Heil, Nathan, & Katul, 2004), and water dispersal (high buoyancy; Nilsson et al., 2010) demonstrates that time since restoration is an important factor for the ecological assessment of restoration effectiveness, and urges restoration planning schemes to include the landscape-scale processes that optimize connectivity with respect to source populations of target species as well (Verhoeven, Soons, Janssen, & Omtzigt, 2008). Moreover, the catchment runoff regime and potential for retention of precipitation and stabilization of stream water supply (cf. Bernhardt & Palmer, 2011) were not restored at the study sites. Prolonged periods of low flow velocities during the growing season, therefore remain likely to occur, potentially stimulating the development of more lentic species and excess vegetation development. Overall, this study demonstrated the effectiveness of a well-coordinated suite of restoration measures to restore river processes and habitat heterogeneity in channelized lowland streams, leading to more typically lotic in-stream vegetation and a more diverse riparian vegetation on the short-term. Additional attention to landscape- and catchment-scale factors, however, is vital for effective ecological recovery.

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AUTHORS' CONTRIBUTIONS

R.G.A.F., C.P., J.T.A.V. and M.B.S. conceived the ideas and designed methodology; R.G.A.F. and C.P. collected the data; R.G.A.F. and C.P. analysed the data; R.G.A.F. led the writing of the manuscript in close cooperation with C.P., J.T.A.V. and M.B.S. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.5874v7h> (Fraaije, Poupin, Verhoeven, & Soons, 2018).

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REFERENCES

- Baatrup-Pedersen, A., Friberg, N., Larsen, S. E., & Riis, T. (2005). The influence of channelisation on riparian plant assemblages. *Freshwater Biology*, 50(7), 1248–1261. <https://doi.org/10.1111/j.1365-2427.2005.01383.x>
- Baatrup-Pedersen, A., Riis, T., Hansen, H. O., & Friberg, N. (2000). Restoration of a Danish headwater stream: Short-term changes in plant species abundance and composition. *Aquatic Conservation-Marine and Freshwater Ecosystems*, 10(1), 13–23. [https://doi.org/10.1002/\(SICI\)1099-0755\(200001/02\)10:1<13::AID-AQC351>3.0.CO;2-S](https://doi.org/10.1002/(SICI)1099-0755(200001/02)10:1<13::AID-AQC351>3.0.CO;2-S)
- Bal, K. D., Bouma, T. J., Buis, K., Struyf, E., Jonas, S., Backx, H., & Meire, P. (2011). Trade-off between drag reduction and light interception of macrophytes: Comparing five aquatic plants with contrasting morphology. *Functional Ecology*, 25(6), 1197–1205. <https://doi.org/10.1111/j.1365-2435.2011.01909.x>
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. Retrieved from <http://CRAN.R-project.org/package=lme4>
- Bernhardt, E. S., & Palmer, M. A. (2011). River restoration: The fuzzy logic of repairing reaches to reverse catchment scale degradation. *Ecological Applications*, 21, 1926–1931. <https://doi.org/10.1890/10-1574.1>
- Biggs, J., Corfield, A., Grøn, P., Hansen, H. O., Walker, D., Whitfield, M., & Williams, P. (1998). Restoration of the rivers Brede, Cole and Skerne: A joint Danish and British EU-LIFE demonstration project, V—Short-term impacts on the conservation value of aquatic macroinvertebrate and macrophyte assemblages. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 8(1), 241–255. [https://doi.org/10.1002/\(SICI\)1099-0755\(199801/02\)8:1<241::AID-AQC269>3.0.CO;2-9](https://doi.org/10.1002/(SICI)1099-0755(199801/02)8:1<241::AID-AQC269>3.0.CO;2-9)
- Bornette, G., & Puijalon, S. (2011). Response of aquatic plants to abiotic factors: A review. *Aquatic Sciences*, 73(1), 1–14. <https://doi.org/10.1007/s00027-010-0162-7>
- Brederveld, R. J., Jähnig, S. C., Lorenz, A. W., Brunzel, S., & Soons, M. B. (2011). Dispersal as a limiting factor in the colonization of restored mountain streams by plants and macroinvertebrates. *Journal of Applied Ecology*, 48(5), 1241–1250. <https://doi.org/10.1111/j.1365-2664.2011.02026.x>
- Brooker, M. P. (1985). The ecological effects of channelization. *The Geographical Journal*, 151(1), 63–69. <https://doi.org/10.2307/633280>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York, NY: Springer.
- Clarke, S. J., & Wharton, G. (2000). An investigation of marginal habitat and macrophyte community enhancement on the River Torne, UK. *Regulated Rivers: Research and Management*, 16(3), 225–244. [https://doi.org/10.1002/\(SICI\)1099-1646\(200005/06\)16:3<225::AID-RRR581>3.0.CO;2-N](https://doi.org/10.1002/(SICI)1099-1646(200005/06)16:3<225::AID-RRR581>3.0.CO;2-N)
- Eekhout, J. P. C., Hoitink, A. J. F., de Brouwer, J. H. F., & Verdonshot, P. F. M. (2015). Morphological assessment of reconstructed lowland streams in the Netherlands. *Advances in Water Resources*, 81, 161–171. <https://doi.org/10.1016/j.advwatres.2014.10.008>
- Ellenberg, H. (1988). *Vegetation ecology of central Europe*. Cambridge: Cambridge University Press.
- Fraaije, R. G. A., Moinier, S., Van Gogh, I., Timmers, R., Van Deelen, J. J., Verhoeven, J. T. A., & Soons, M. B. (2017). Spatial patterns of water-dispersed seed deposition along strong riparian gradients. *PLoS ONE*, 12(9), e0185247. <https://doi.org/10.1371/journal.pone.0185247>
- Fraaije, R. G. A., Poupin, C., Verhoeven, J. T. A., & Soons, M. B. (2018). Data from: Functional responses of aquatic and riparian vegetation to hydrogeomorphic restoration of channelized lowland streams and their valleys. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.5874v7h>
- Fraaije, R. G. A., ter Braak, C. J. F., Verduyn, B., Breeman, L. B. S., Verhoeven, J. T. A., & Soons, M. B. (2015). Early plant recruitment stages set the template for the development of vegetation patterns along a hydrological gradient. *Functional Ecology*, 29(7), 971–980. <https://doi.org/10.1111/1365-2435.12441>
- Fraaije, R. G. A., ter Braak, C. J. F., Verduyn, B., Verhoeven, J. T. A., & Soons, M. B. (2015). Dispersal versus environmental filtering in a dynamic system: Drivers of vegetation patterns and diversity along stream riparian gradients. *Journal of Ecology*, 103(6), 1634–1646. <https://doi.org/10.1111/1365-2745.12460>
- Haase, P., Hering, D., Jähnig, S. C., Lorenz, A. W., & Sundermann, A. (2013). The impact of hydromorphological restoration on river ecological status: A comparison of fish, benthic invertebrates, and macrophytes. *Hydrobiologia*, 704(1), 475–488. <https://doi.org/10.1007/s10750-012-1255-1>
- Harvey, G. L., Clifford, N. J., & Gurnell, A. M. (2008). Towards an ecologically meaningful classification of the flow biotope for river inventory, rehabilitation, design and appraisal purposes. *Journal of Environmental Management*, 88(4), 638–650. <https://doi.org/10.1016/j.jenvman.2007.03.039>
- Helfield, J. M., Capon, S. J., Nilsson, C., Jansson, R., & Palm, D. (2007). Restoration of rivers used for timber floating: Effects on riparian plant diversity. *Ecological Applications*, 17(3), 840–851. <https://doi.org/10.1890/06-0343>
- Hering, D., Aroviita, J., Baatrup-Pedersen, A., Brabec, K., Buijse, T., Ecke, F., ... Kail, J. (2015). Contrasting the roles of section length and instream habitat enhancement for river restoration success: A field study of 20 European restoration projects. *Journal of Applied Ecology*, 52(6), 1518–1527. <https://doi.org/10.1111/1365-2664.12531>
- Hill, M. O., Mountford, J. O., Roy, D. B., & Bunce, R. G. H. (1999). *Ellenberg's indicator values for British plants*. Huntingdon: Institute of Terrestrial Ecology.
- Hunt, R., Hodgson, J. G., Thompson, K., Bungener, P., Dunnett, N. P., & Askew, A. P. (2004). A new practical tool for deriving a functional signature for herbaceous vegetation. *Applied Vegetation Science*, 7(2), 163–170. [https://doi.org/10.1658/1402-2001\(2004\)007\[0163:anptfd\]2.0.co;2](https://doi.org/10.1658/1402-2001(2004)007[0163:anptfd]2.0.co;2)
- Jähnig, S. C., Brabec, K., Buffagni, A., Erba, S., Lorenz, A. W., Ofenböck, T., ... Hering, D. (2010). A comparative analysis of restoration measures and their effects on hydromorphology and benthic invertebrates in 26 central and southern European rivers. *Journal of Applied Ecology*, 47(3), 671–680. <https://doi.org/10.1111/j.1365-2664.2010.01807.x>
- Jähnig, S. C., Brunzel, S., Gacek, S., Lorenz, A. W., & Hering, D. (2009). Effects of re-braiding measures on hydromorphology, floodplain vegetation, ground beetles and benthic invertebrates in mountain rivers. *Journal of Applied Ecology*, 46(2), 406–416. <https://doi.org/10.1111/j.1365-2664.2009.01611.x>
- Januschke, K., Brunzel, S., Haase, P., & Hering, D. (2011). Effects of stream restorations on riparian mesohabitats, vegetation and carabid beetles. *Biodiversity and Conservation*, 20(13), 3147–3164. <https://doi.org/10.1007/s10531-011-0119-8>
- Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., ... Peco, B. (2008). The LEDA Traitbase: A database of life-history traits of the Northwest European flora. *Journal of Ecology*, 96, 1266–1274. <https://doi.org/10.1111/j.1365-2745.2008.01430.x>
- Kuglerová, L., Botková, K., & Jansson, R. (2017). Responses of riparian plants to habitat changes following restoration of channelized streams. *Ecohydrology*, 10(1), e1798. <https://doi.org/10.1002/eco.1798>

- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, 82(13), 1–26. <https://doi.org/10.18637/jss.v082.i13>
- Lorenz, A. W., Korte, T., Sundermann, A., Januschke, K., & Haase, P. (2012). Macrophytes respond to reach-scale river restorations. *Journal of Applied Ecology*, 49(1), 202–212. <https://doi.org/10.1111/j.1365-2664.2011.02082.x>
- Lüderitz, V., Speierl, T., Langheinrich, U., Völkl, W., & Gersberg, R. M. (2011). Restoration of the Upper Main and Rodach rivers – The success and its measurement. *Ecological Engineering*, 37(12), 2044–2055. <https://doi.org/10.1016/j.ecoleng.2011.07.010>
- Madsen, J. D., Chambers, P. A., James, W. F., Koch, E. W., & Westlake, D. F. (2001). The interaction between water movement, sediment dynamics and submersed macrophytes. *Hydrobiologia*, 444(1–3), 71–84. <https://doi.org/10.1023/A:1017520800568>
- Malmqvist, B., & Rundle, S. (2002). Threats to the running water ecosystems of the world. *Environmental Conservation*, 29(2), 134–153. <https://doi.org/10.1017/S0376892902000097>
- Meyer, A., Combroux, I., Schmitt, L., & Trémoilières, M. (2013). Vegetation dynamics in side-channels reconnected to the Rhine River: What are the main factors controlling communities trajectories after restoration? *Hydrobiologia*, 714(1), 35–47. <https://doi.org/10.1007/s10750-013-1512-y>
- Myers, J. A., Chase, J. M., Crandall, R. M., & Jiménez, I. (2015). Disturbance alters beta-diversity but not the relative importance of community assembly mechanisms. *Journal of Ecology*, 103(5), 1291–1299. <https://doi.org/10.1111/1365-2745.12436>
- Naiman, R. J., & Décamps, H. (1997). The ecology of interfaces: Riparian zones. *Annual Review of Ecology and Systematics*, 28, 621–658. <https://doi.org/10.1146/annurev.ecolsys.28.1.621>
- Nilsson, C., Brown, R. L., Jansson, R., & Merritt, D. M. (2010). The role of hydrochory in structuring riparian and Wetland vegetation. *Biological Reviews*, 85(4), 837–858. <https://doi.org/10.1111/j.1469-185X.2010.00129.x>
- Nilsson, C., Polvi, L. E., Gardeström, J., Hasselquist, E. M., Lind, L., & Sarneel, J. M. (2015). Riparian and in-stream restoration of boreal streams and rivers: Success or failure? *Ecohydrology*, 8(5), 753–764. <https://doi.org/10.1002/eco.1480>
- Noon, K. F. (1996). A model of created wetland primary succession. *Landscape and Urban Planning*, 34(2), 97–123. [https://doi.org/10.1016/0169-2046\(95\)00209-X](https://doi.org/10.1016/0169-2046(95)00209-X)
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., ... Wagner, H. (2015). vegan: Community ecology package. R package version 2.2-1. Retrieved from <http://CRAN.R-project.org/package=vegan>
- Pedersen, M. L., Andersen, J. M., Nielsen, K., & Linnemann, M. (2007). Restoration of Skjern River and its valley: Project description and general ecological changes in the project area. *Ecological Engineering*, 30(2), 131–144. <https://doi.org/10.1016/j.ecoleng.2006.06.009>
- Pedersen, T. C. M., Baattrup-Pedersen, A., & Madsen, T. V. (2006). Effects of stream restoration and management on plant communities in lowland streams. *Freshwater Biology*, 51(1), 161–179. <https://doi.org/10.1111/j.1365-2427.2005.01467.x>
- Riis, T. (2008). Dispersal and colonisation of plants in lowland streams: Success rates and bottlenecks. *Hydrobiologia*, 596(1), 341–351. <https://doi.org/10.1007/s10750-007-9107-0>
- Riis, T., & Biggs, B. J. F. (2003). Hydrologic and hydraulic control of macrophyte establishment and performance in streams. *Limnology and Oceanography*, 48(4), 1488–1497. <https://doi.org/10.4319/lo.2003.48.4.1488>
- Rohde, S., Schütz, M., Kienast, F., & Englmaier, P. (2005). River widening: An approach to restoring riparian habitats and plant species. *River Research and Applications*, 21(10), 1075–1094. <https://doi.org/10.1002/rra.870>
- Silvertown, J., Araya, Y., & Gowing, D. (2015). Hydrological niches in terrestrial plant communities: A review. *Journal of Ecology*, 103(1), 93–108. <https://doi.org/10.1111/1365-2745.12332>
- Smiley, P. C., King, K. W., & Fausey, N. R. (2011). Influence of herbaceous riparian buffers on physical habitat, water chemistry, and stream communities within channelized agricultural headwater streams. *Ecological Engineering*, 37(9), 1314–1323. <https://doi.org/10.1016/j.ecoleng.2011.03.020>
- Soons, M. B., de Groot, G. A., Cuesta Ramirez, M. T., Fraaije, R. G. A., Verhoeven, J. T. A., & de Jager, M. (2017). Directed dispersal by an abiotic vector: Wetland plants disperse their seeds selectively to suitable sites along the hydrological gradient via water. *Functional Ecology*, 31(2), 499–508. <https://doi.org/10.1111/1365-2435.12771>
- Soons, M. B., Hefting, M. M., Dorland, E., Lamers, L. P. M., Versteeg, C., & Bobbink, R. (2017). Nitrogen effects on plant species richness in herbaceous communities are more widespread and stronger than those of phosphorus. *Biological Conservation*, 212, 390–397. <https://doi.org/10.1016/j.biocon.2016.12.006>
- Soons, M. B., Heil, G. W., Nathan, R., & Katul, G. G. (2004). Determinants of long-distance seed dispersal by wind in grasslands. *Ecology*, 85(11), 3056–3068. <https://doi.org/10.1890/03-0522>
- van der Meijden, R. (2005). *Heukels' Flora van Nederland Drieëntwintigste Druk*. Groningen: Wolters-Noordhoff.
- Verdonschot, P. F. M., & Nijboer, R. C. (2002). Towards a decision support system for stream restoration in the Netherlands: An overview of restoration projects and future needs. *Hydrobiologia*, 478(1–3), 131–148. <https://doi.org/10.1023/A:1021026630384>
- Verhoeven, J. T. A., Soons, M. B., Janssen, R., & Omtzigt, N. (2008). An Operational Landscape Unit approach for identifying key landscape connections in wetland restoration. *Journal of Applied Ecology*, 45(5), 1496–1503. <https://doi.org/10.1111/j.1365-2664.2008.01534.x>
- Wisheu, I. C., & Keddy, P. A. (1992). Competition and centrifugal organization of plant communities – Theory and tests. *Journal of Vegetation Science*, 3(2), 147–156. <https://doi.org/doi:10.2307/3235675>
- Wood, P. J., & Armitage, P. D. (1997). Biological effects of fine sediment in the lotic environment. *Environmental Management*, 21(2), 203–217. <https://doi.org/10.1007/s002679900019>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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