

Plants living on the edge

**Colonization processes of aquatic and riparian vegetation
along restored lowland streams**

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Plants living on the edge: colonization processes of aquatic and
riparian vegetation along restored lowland streams

Planten die op de rand leven: kolonisatie processen van beek- en oevervegetatie
langs herstelde laaglandbeken

(met een samenvatting in het Nederlands)

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Chapter 1

General Introduction

PLANT SPECIES DISTRIBUTIONS AND BIODIVERSITY

Plant diversity is increasingly threatened across the globe by habitat loss and deterioration (Tilman *et al.* 2001; Dirzo & Raven 2003; Butchart *et al.* 2010). Besides threats to the conservation of species (Myers *et al.* 2000), these biodiversity declines may impair ecosystem functioning and stability (Tilman & Downing 1994; McCann 2000; Tilman *et al.* 2012). In order to successfully protect sensitive species and biodiversity in general, a central goal in ecology is to understand the mechanisms that determine species distributions and biodiversity.

Determinants of species distributions and biodiversity

Niche differentiation is a major concept in this field, explaining species distributions by interspecific differences in the ability to acquire limiting resources (Tilman 1982) or withstand adverse conditions (Kenkel *et al.* 1991; Lenssen & de Kroon 2005). This combination of abiotic constraints and biotic interactions forms an 'environmental filter' (*sensu* van der Valk 1981; Keddy 1992; ter Steege & Zagt 2002) for species establishment and persistence, which segregates species along environmental or temporal niches (Silvertown 2004). With every species occupying its own niche, stable coexistence in an ecosystem is promoted which generally increases biodiversity.

A concept contrasting to niche differentiation by environmental filtering, is the explanation of species distribution by differences in arrival, or 'dispersal filtering'. According to this view, size of the local and regional species pools, chance colonization events and differences in species dispersal abilities are critical factors structuring plant communities, with species being 'neutral' to differences in habitat conditions (MacArthur & Wilson 1967; Zobel 1997; Hubbell 2001; Myers & Harms 2009).

Mechanisms of environmental and dispersal filtering

Although there is general consensus that both environmental filtering and dispersal filtering play a role in natural community assemblages (Gravel *et al.* 2006; Adler *et al.* 2007; Myers & Harms 2009; Götzenberger *et al.* 2012; Fig. 1.1), the assessment of their relative importance across time, space, or ecosystem types remains challenging (Chase & Myers 2011; Shipley *et al.* 2012). Moreover, although niche differentiation along environmental axes has been shown in many studies (Silvertown 2004) it is often unclear at which stage in a plant's life cycle such filters operate: during early stages, thereby preventing occupation of the full potential niche of adult plants (Grubb 1977; Grime 2001), or at later stages, e.g. through competitive interactions among adults (Wedin & Tilman 1993). Additionally, several early recruitment processes can be distinguished, namely germination, seedling survival and seedling growth. While early recruitment stages are increasingly recognized as determinants of adult species distributions (Evans & Etherington 1990; Eriksson & Ehrlén 1992; Kotorová & Lepš

1999; Stampfli & Zeiter 2008), studies to date have focused either on one particular recruitment stage or on the combined result of all stages (total seedling establishment). Hence, quantitative information on the relative importance of the different stages to recruitment and adult species distributions is generally lacking. Such information would add significantly to our understanding of community assembly and biodiversity.

Also for dispersal filtering several mechanisms may play a role. Dispersal limitation may occur due to a lack of nearby source populations (Bakker & Berendse 1999; Brederveld *et al.* 2011; Baattrup-Pedersen *et al.* 2013; Lorenz & Feld 2013), by limited dispersal opportunities (blocked dispersal pathways; Ozinga *et al.* 2009; Nilsson *et al.* 2010), but also by a mismatch in spatial patterns of deposited seeds hampering seeds in reaching certain microhabitats (Nathan & Muller-Landau 2000; Jordano *et al.* 2007; Sarneel & Soons 2012; Sarneel *et al.* 2014a). A better understanding of plant dispersal pathways is required to be able to predict species (re-)colonization potential and their effects on plant diversity.

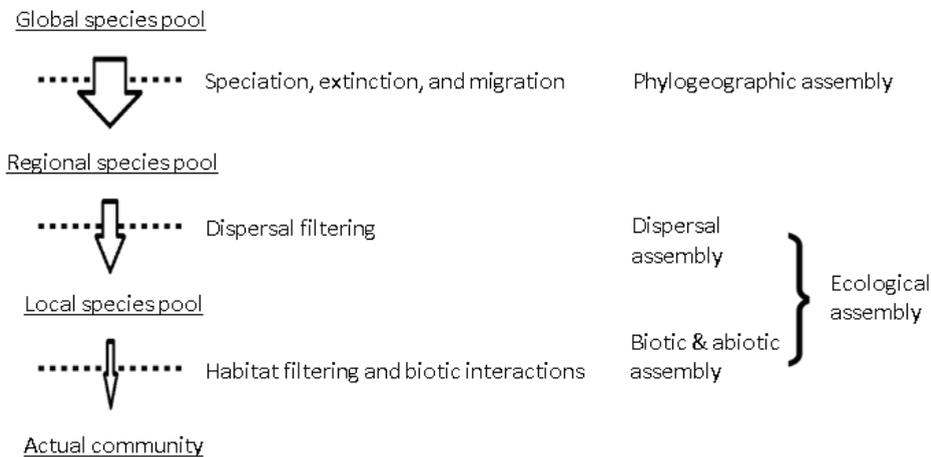


Figure 1.1. Overview of the processes that determine plant community assembly (modified from Götzenberger *et al.* 2012). The global species pool defines a regional species pool through the speciation, extinction and migration of species (phylogeographic assembly). At a given local site the species pool constitutes species from the regional species pool that are able to disperse there (dispersal assembly). At the local site, habitat filtering and biotic interactions define the actual assemblage of plant species (ecological assembly).

Relative importance of environmental and dispersal filtering in dynamic habitats

Recent studies suggest that environment-driven community assembly may become more important under stressful environmental conditions (Chase 2007; Jiang & Patel 2008; Lepori & Malmqvist 2009), whereas dispersal filtering may become more prevalent under benign conditions (Myers & Harms 2009; Germain *et al.* 2013). Species interactions may additionally enforce both types of filtering by competitive displacement of subordinates towards peripheral ends of environmental gradients (Wisheu & Keddy 1992), narrowing species' realized niche ranges (Hutchinson 1957; Pickett & Bazzaz 1978; Silvertown *et al.* 1999), or by preventing establishment of later arriving species ('priority effects'), especially in more productive environments (Chase 2010; Kardol *et al.* 2013).

In dynamic habitats that are prone to natural disturbance regimes, it is particularly unclear whether environmental filtering or dispersal filtering dominates, or how the two interact in community assembly (Lepori & Malmqvist 2009; Myers & Harms 2009; Brederveld *et al.* 2011). Disturbance regimes, i.e. "any relatively discrete event that disrupts the structure of an ecosystem, community, or population, and changes resource availability or the physical environment" (White & Pickett 1985), are an intrinsic feature of many highly diverse and ecologically important habitats, that are increasingly disrupted by human interventions across the globe (Mack & D'Antonio 1998; Shea *et al.* 2004; Turner 2010). Information on the relative importance of dispersal filtering versus environmental filtering is of highest importance for the design of effective conservation and restoration strategies of these habitats. When environmental filtering dominates, measures should first seek to improve or maintain proper local environmental conditions (e.g. Roelofs *et al.* 2002; Jähnig *et al.* 2009; Lamers *et al.* 2015) but when dispersal filtering dominates, it is of primary importance to protect nearby source populations and secure dispersal pathways (Soons *et al.* 2005; Verhoeven *et al.* 2008; Brederveld *et al.* 2011)

STREAMS AND THEIR RIPARIAN ZONES

Riparian zones along streams provide a typical example of a dynamic and highly diverse habitat (Naiman & Décamps 1997), in which the relative roles of dispersal filtering and environmental filtering, as well as a full mechanistic understanding of both filtering processes, are yet unresolved. Riparian zones form the interface between the aquatic and terrestrial environments, and comprise the area between the low and (extremely) high water marks (Naiman & Décamps 1997). Spatial and temporal variation in flooding (limitation by abiotic stress) and drought (resource limitation) stimulate community re-assembly and impose strong environmental filters. These dynamics coincide with a strong hydrological gradient from the channel to the upland, together generating gradients in the vegetation that are commonly explained by species niche

separation (more specifically, their 'hydrological niches'; Silvertown *et al.* 1999). Vegetation patterns along riparian gradients may be induced by abiotic constraints on recruitment stages (Keddy & Ellis 1985; Hölzel & Otte 2003; van Eck *et al.* 2004) but also during adult stages (Squirres & van der Valk 1992), as well as by interspecific competition among adult plants (Grace & Wetzel 1982; Kotowski *et al.* 2006). Hence, it remains difficult to evaluate how (and how much) recruitment processes, or their separate stages, contribute to the high biodiversity and commonly observed gradients found in vegetation along stream riparian zones (Naiman & Décamps 1997; Pollock *et al.* 1998; Ward 1998).

The generally high propagule arrival in riparian zones supports the potential role of environmental filtering. These propagules arrive via several dispersal vectors, including wind (anemochory), animals (zoochory), and water (hydrochory) (Soons 2006; Nilsson *et al.* 2010; Soomers *et al.* 2013). Hydrochory has been shown to be the dominant dispersal vector in riparian habitats, occurring over long distances (up to 152.5 km for seed mimics; Andersson *et al.* 2000), effectively adding propagules of new species into existing vegetation (Gurnell *et al.* 2008) and to newly created river banks (Gurnell *et al.* 2006; Chapter 2). Uncertainties remain, however, on the elevational distribution patterns of deposited seeds along the riparian gradients, as this position is influenced by complex interactions between extrinsic factors (e.g., stream discharge patterns, flow velocity, water levels and channel roughness) and intrinsic factors (e.g., seed buoyancy, seed shape and timing of seed release; Nilsson *et al.* 2010). Several studies have shown that arrival of plant propagules (either seeds or vegetative fragments) along stream riparian zones is controlled strongly by spatially and temporally highly variable flooding events (Boedeltje *et al.* 2004; Moggridge *et al.* 2009; Chapter 2). These patterns may be very important to subsequent vegetation development (e.g. Andersson *et al.* 2000), and may lead to priority effects in certain locations along the riparian gradients (blocking establishment of later arriving species) in riparian community assembly (J.M. Sarneel *et al.*, unpublished data). This suggests an important role for dispersal filtering to community assembly along riparian gradients as well.

Channelization

Understanding the regulation of species distribution and diversity, is increasingly urgent for streams and riparian zones. Many streams worldwide have been impacted by modifications for the purpose of flood control, drinking-water abstraction, and agricultural activities (Brookes *et al.* 1983; Brookes 1987; Mattingly *et al.* 1993; Malmqvist & Rundle 2002). More than 90% of all lowland streams in the Netherlands, Denmark and Britain have been channelized between 1920 and 1970 (Brookes 1987; Brookes & Long 1990; Verdonschot & Nijboer 2002). In the Netherlands, where lowland

streams occur in the southern and eastern part directly upstream of the Rhine-Meuse delta, even 96% is affected by changes relating to channelization. The remaining 4% is near natural, but still indirectly affected by pollution, groundwater extraction or land use changes in the catchment, and primarily occurs in the upper courses of streams (Verdonschot & Nijboer 2002).

Because of the morphological and hydrological changes following channelization and increased drainage, these modified streams are often deeply incised and wider and deeper (Brookes 1988), with a narrower and steeper riparian corridor compared to natural streams. The lower stream levels consequently lead to lower water tables adjacent to the stream (Hardison *et al.* 2009) and to less frequent overbank flows, because the channel's discharge capacity is increased. This causes drought in the riparian corridor and a reduction of the floodplain area (Fig. 1.2). As summarized by Ward (1998), the hydrogeomorphic changes caused by channelization decrease the spatiotemporal heterogeneity and connectivity, which ultimately leads to a reduced biodiversity (Table 1.1).

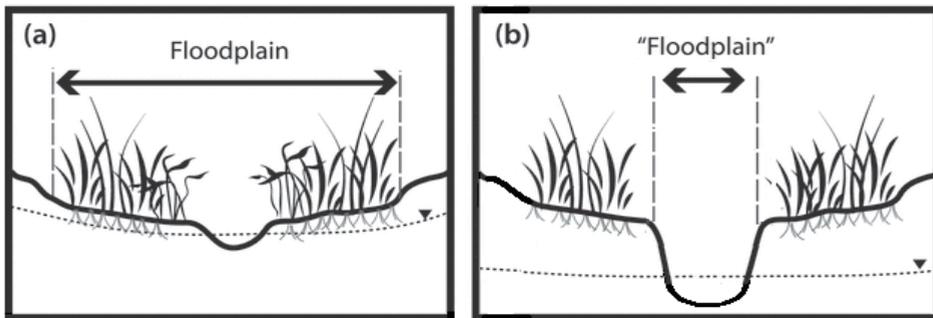


Figure 1.2. Cross-sectional view of (a) natural streams with high water tables and wide floodplains and (b) channelized streams with lower water tables and strongly reduced floodplains, modified from Hardison *et al.* (2009).

Table 1.1. Effects of channelization on the spatio-temporal heterogeneity and connectivity of stream ecosystems

	Channelized streams compared to natural streams
Environmental gradients	Much shorter and steeper moisture gradient
Natural disturbance regimes	Lower disturbance because no overbank flow, less variation in sedimentation, erosion and flow velocity
Connectivity	Lower lateral connectivity, reduction of floodplain
Abiotic conditions	Overall less habitat heterogeneity

Stream restoration measures

To improve the ecological value and biodiversity, many stream restoration projects have been undertaken in the last two decades, with 'digging of meanders' and 'increase of water retention' as the most frequently applied measures (Verdonschot & Nijboer 2002). Ecological improvement, however, lags behind in many projects, with contamination, diffuse sources of pollution, spatial limitations and fragmented approaches as main causes (Verdonschot & Nijboer 2002). In many restoration projects attention was primarily given to stream morphology, while inundation of the adjacent valley was not restored. Natural disturbance regimes and moisture gradients were addressed too indirectly, so that these remained largely unrestored. In other cases stream width and depth have been badly designed with respect to their dimensions, resulting in too little inundation or too low stream discharge at base flows, culminating in the accumulation of fine sediments. In most projects, natural inundation regimes and moisture gradients were hardly considered, so that habitat heterogeneity only marginally changed.

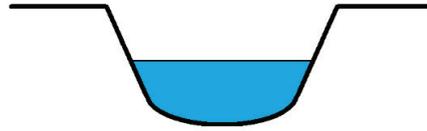
Innovative stream restoration

New innovative restoration measures which combine changes in morphology and hydrology are expected to be more promising in restoring ecological values. The main objective of these measures is to increase flow velocity at base flows, decrease flow velocity during peak flows and restore the natural inundation regime, by adjusting the morphology of the stream profile (Fig. 1.3). To achieve this, riparian corridors were widened and made less steep, and were allowed to inundate more frequently because the stream bed bottom was more strongly raised than in earlier restoration projects. As a consequence, higher water tables and increased inundation led to restored moisture gradients, thereby improving the conditions for wetland vegetation (Mountford & Chapman 1993; Stromberg *et al.* 1996; Clarke & Wharton 2000). Overly slow flows during low discharges were avoided by narrow stream beds, while increased water retention was realized at high discharges, because of the increased space for inundation. This was combined with meandering which increased geomorphological variations (Fig. 1.3).

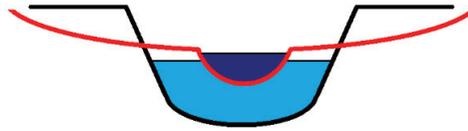
The main goals of the innovative restoration measures can roughly be divided in factors that directly affect the environmental conditions of the stream and factors that affect the conditions of the riparian zone. The main effects of the restoration measures relevant for vegetation development are summarized in Table 1.2.



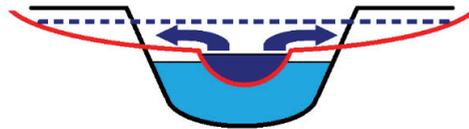
Channelized stream



Restored base flow: shallow and narrow



Restored peak flow: space for inundation



Re-meandering increases heterogeneity

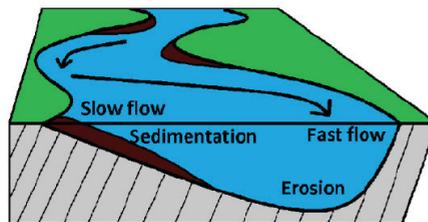


Figure 1.3. Visualization of the innovative restoration measures with a newly created transversal profile of the stream and riparian zone (indicated in red) resulting in a raised stream bed, a narrow stream during base flow and room for inundation during peak flow. Meandering of the watercourse contributed to in-stream and riparian habitat heterogeneity, with spatial variation in flow velocities leading to increased sedimentation and creation of sand banks in inner bends, and erosion and undercutting in outer bends.

Table 1.2. Major effects of the innovative restoration measures on the stream and riparian zone

	Effects on the stream and riparian zone
Riparian zone	Increased winter inundation
Riparian zone	Higher water tables
Riparian zone	Wider floodplains with wider moisture gradients
Stream	Smaller seasonal differences in flow velocities
Stream	Increased spatial variation in flow velocities
Stream	A more narrow and shallow stream

THIS THESIS

Research objective

This research aimed at identifying the most important drivers of plant species distribution and diversity patterns along streams and their riparian zones, and at assessing ecological responses to innovative restoration measures. Particular attention was given to the relative importance of dispersal versus environmental filtering, and on the role of early stages during environmental filtering, including germination, seedling survival and seedling growth, for adult distribution patterns and diversity. By studying these processes along recently restored lowland streams and riparian zones, I aimed to gain better insight in their community assembly and diversity development, and provide recommendations for future conservation and restoration of these potentially highly diverse, but nowadays strongly deteriorated ecosystems. In particular, this research addressed which conditions lead to a high biodiversity and the return of typical aquatic and riparian plant species. Crucial factors that stimulate or hamper the development of desired species were identified.

Newly created riparian zones, which are cleared of vegetation, provided an ideal environment to investigate some of the fundamental knowledge gaps on the determination of species distribution patterns and species coexistence. The bare substrate of the restored stream reaches made it possible to study patterns in the initial arrival of seeds, and assess the relative importance of these patterns (dispersal filtering) compared to patterns in three different recruitment stages (germination, seedling survival and seedling growth; environmental filtering), for determining adult distribution patterns in the early successional vegetation along restored stream riparian gradients. Comparing the developing vegetation at restored stream reaches to that of nearby unrestored (still channelized) stream reaches allowed me to study the ecological responses to the abiotic changes by the innovative restoration measures, and provide information on trajectories of recovery following such strong interventions by hydrogeomorphic restoration.

Study sites

Five lowland streams were selected to study aquatic and riparian vegetation colonization after stream restoration. These included the Hagmolenbeek (HM), Hooge Raam (HR), Kleine Aa (KA), Luntersche Beek (LB) and Tungalroyse beek (TR). All streams are located in the Pleistocene areas in the central, eastern, and southern parts of the Netherlands with soil surfaces dominantly consisting of Aeolian sand deposits (Fig. 1.4). The streams are classified as slow flowing streams (flow velocity $< 0.5 \text{ m s}^{-1}$) except HR which is classified as a fast flowing stream (van der Molen *et al.* 2012). At all streams, reaches of 0.8-2 km stream length were restored between 2009 and 2011. Hydrogeomorphic restoration was most pronounced at HM, where channel width decreased from 8.7 to 2.8 m, channel depth from 0.9 to 0.4 m, and riparian zone width increased from 2.2 to 15.3 m (Table 1.3). HR differed from the other study locations as channel width was increased instead of decreased by restoration and no meandering of the watercourse was applied.

Vegetation was allowed to colonize naturally at all streams. Only at HM, the riparian zones were sown with with a seed mixture of *Lolium perenne*, *Trifolium repens*, and *Phleum pratense* subsp. *pratense* (van der Meijden 2005), to reduce possible erosion after restoration. Vegetation management of the restored reaches differed between the study locations. Yearly mowing was applied at HM (aquatic and riparian vegetation) and at KA (riparian vegetation). No mowing occurred at HR and TR as a forested riparian zone was targeted, and no mowing occurred yet at LB and in the channels of KA because vegetation development was still relatively sparse in the first years after restoration.

Table 1.3. Characteristics of the study locations Hagmolenbeek (HM), Hooge Raam (HR), Kleine Aa (KA), Luntersche beek (LB) and Tungalroyse beek (TR), for restored reaches (R) and unrestored reaches (U). Channel depths are representative for the central parts of the channel and discharge values apply to the year 2012, except discharge values at KA (March 2013–December 2013).

	HM		HR		KA		LB		TR	
	R	U	R	U	R	U	R	U	R	U
Channel width (m)	2.8	8.7	8.3	5.0	7.7	9.3	5.5	6.7	9.8	9.9
Channel depth (m)	0.4	0.9	0.3	0.3	1.1	1.7	0.2	0.9	1.0	1.2
Riparian width (m)	15	2	15	2	12	3	11	3	14	2
Avg. hourly discharge ($\text{m}^3 \text{ s}^{-1}$)	0.1		0.2		0.9		0.4		1.1	
Peak discharge ($\text{m}^3 \text{ s}^{-1}$)	1.0		1.6		7.2		6.5		5.0	

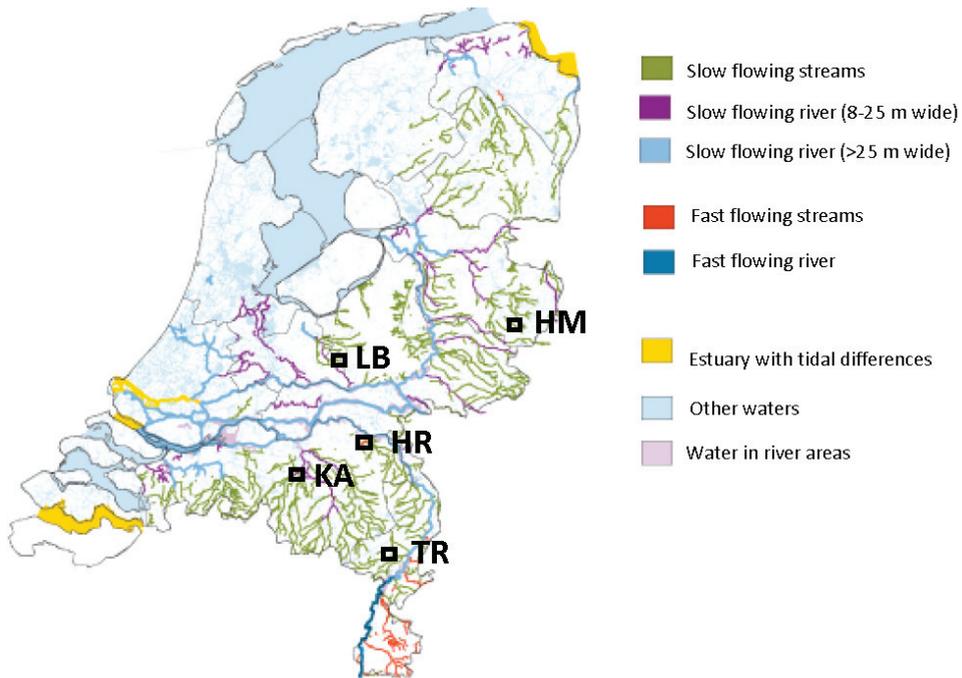


Figure 1.4. Locations of the five study areas in the Netherlands, including the Hagmolenbeek (HM), Hooge Raam (HR), Kleine Aa (KA), Luntersche beek (LB) and Tungelroyse beek (TR). The map displays all running waters in the Netherlands, categorized in different types based on van der Molen *et al.* (2012), with ‘slow flowing’ representing flow velocities below 0.5 m s^{-1} and ‘fast flowing’ flow velocities above it. Picture modified from CBS *et al.* (2014).

Thesis outline

In this thesis, I aimed to unravel the importance of the early stages in vegetation development, including arrival of seeds, germination, seedling survival, and seedling growth, to adult distribution patterns along stream riparian gradients. Moreover, the effects of specific target factors in restoration for aquatic and riparian vegetation development were studied. Study approaches consisted of field monitoring of seed deposition patterns, field experiments on recruitment of seeds and seedlings (at only the restored reaches), and of field monitoring of the aquatic and riparian vegetation in the first years after restoration (both at restored and unrestored reaches). The thesis follows a line from the earliest stages to later stages in vegetation development as visualized in Figure 1.5.

Chapter 2 addresses the elevational patterns of hydrochorous seed deposition along riparian gradients. At three study locations (all restored reaches), seed traps were pinned to the ground to monitor natural seed rain along the entire

riparian gradient. Identity and quantity of seeds were determined in the laboratory and, together with their trait values (e.g. seed buoyancy, seed density) linked to the hydrological conditions at the seed traps along the riparian gradients.

In **Chapter 3** field experiments were performed on germination, seedling survival and seedling growth of 17 native riparian plant species common to north-west Europe (Table 1) by introducing their seeds and seedlings across hydrological gradients in the riparian zones of three restored lowland streams. Their performance was related to indicator values for their adult distribution optima.

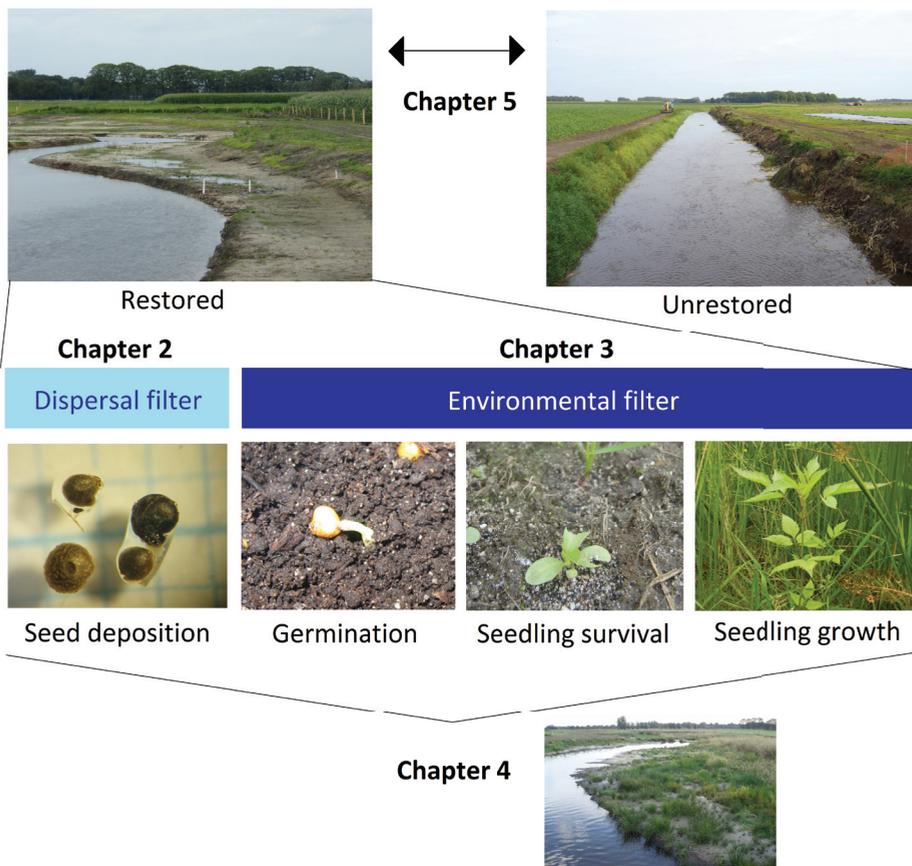


Figure 1.5. Overview of the ecosystems and processes studied. In the riparian zone of restored reaches patterns in the arrival of seeds (Chapter 2), the relative importance of germination, seedling survival and seedling growth to niche segregation (Chapter 3), and the relative importance of arrival versus recruitment to adult distribution patterns (Chapter 4) were studied. In Chapter 5 the aquatic and riparian vegetation of restored stream reaches was compared with nearby unrestored stream reaches.

Chapter 4 focuses on the relative importance of dispersal filtering versus environmental filtering for species distribution and diversity patterns along hydrological gradients of stream riparian zones. Natural seed arrival patterns of aquatic and riparian plant species were measured in riparian zones at three restored lowland streams in the Netherlands (Chapter 2). Simultaneously, for 17 riparian plant species common to north-western Europe, patterns in germination, seedling survival and seedling growth were measured by introducing their seeds and seedlings along these gradients (Chapter 3). For overlapping species, patterns in seed arrival (dispersal filter) and patterns in germination, seedling survival and seedling growth (environmental filter) were analysed considering their relative contributions to plant species distribution in the natural developing vegetation 1 and 2 years after restoration.

In **Chapter 5** the vegetation of innovatively restored reaches was compared to that of nearby unrestored reaches of five lowland streams. Physicochemical variables were assessed along complete stream valley transversal profiles (cross-sections) and related to responses of aquatic and riparian vegetation, focusing on diversity metrics, and responses of plant species grouped per growth form and per indicator value for moisture.

In **Chapter 6** a synthesis is presented of Chapters 2-5, and the results are placed in the context of fundamental insights in species distribution and diversity, and restoration of streams and their riparian zones. The results are translated to recommendations for maximal ecological improvement by stream restoration measures.



Chapter 2

Elevational patterns of hydrochorous seed deposition along stream riparian gradients

Rob G.A. Fraaije, Sophie Moinier, Iris van Gogh, Robert Timmers,
Joost J. van Deelen, Jos T.A. Verhoeven and Merel B. Soons

ABSTRACT

Riparian ecosystems along streams are among the most heavily degraded and most frequently restored ecosystems worldwide. They naturally harbour a high plant diversity, with many increasingly endangered species. In our current heavily modified and fragmented catchments, many of these species are sensitive to dispersal limitation. Better understanding of riparian plant dispersal pathways is required to predict species (re-)colonization potential and improve success rates of stream and riparian zone conservation and restoration activities.

Dispersal by water (hydrochory) is an important mechanism for (long-distance) dispersal of riparian species, but also a determinant of the position along the riparian hydrological gradient where seeds become deposited. Due to the complex interplay between environmental factors and species traits, and the difficulties in separating hydrochorous from non-hydrochorous seed deposition, it remains unclear how exactly hydrochory contributes to seed deposition patterns and subsequent plant recruitment success.

We compared hydrochorous and non-hydrochorous seed deposition, and quantified patterns of seed deposition. We did this in newly created riparian zones, devoid of any vegetation just after construction, which provide an ideal environment to study seed deposition along riparian gradients. We monitored water levels and measured seed deposition with seed traps along the full range of riparian hydrological conditions (from permanently flooded to never flooded). For each seed trap we analysed the numbers of seeds and species, community composition and community-weighted means of seed and species traits related to hydrochory.

Average seed numbers and species richness were significantly higher in flooded seed traps than in non-flooded seed traps. Seed and plant traits in flooded traps suggest a greater reliance on hydrochory, with higher seed buoyancies and plant Ellenberg F-values, and lower seed specific weights than seeds of non-flooded seed traps. In more detail, we found a gradually decreasing concentration of water-dispersed seeds from the channel to the upland, with a peak of highly buoyant seeds at the average water line, and clear elevational sorting of non-buoyant seeds within the floodplain.

These results establish a critical role of hydrochorous dispersal in patterns of seed deposition along the riparian gradient, and imply that natural flooding regimes form a key process to restore in riparian zones. These floods deliver many seeds of typical riparian species and often deposit them at species-specific favourable hydrological microhabitats.

INTRODUCTION

Plant diversity is threatened across the globe by habitat loss and deterioration (Tilman *et al.* 2001; Dirzo & Raven 2003; Butchart *et al.* 2010). In response, restoration projects are carried out to counteract species losses. Unfortunately, successful restoration of abiotic site conditions does frequently not result in re-establishment of desired species (e.g., Bischoff 2002; Jähnig *et al.* 2009; Brederveld *et al.* 2011). Re-colonization by plant species may be hampered either by some (unknown) abiotic or biotic site condition, or simply because species are not able to reach the restored site. The latter is often due to a lack of nearby source populations (Bakker & Berendse 1999; Baattrup-Pedersen *et al.* 2013; Lorenz & Feld 2013), to limited dispersal opportunities, and/or a mismatch in spatial patterns of deposited seeds hampering seeds in reaching certain microhabitats (Nathan & Muller-Landau 2000; Jordano *et al.* 2007; Sarneel & Soons 2012; Sarneel *et al.* 2014a). A better understanding of plant dispersal pathways is required to be able to predict species (re-)colonization potential and to improve success rates of restoration activities. This applies particularly to riparian ecosystems along streams and rivers, which are among the most heavily degraded ecosystems (Malmqvist & Rundle 2002) and among the most frequently restored (Verdonschot & Nijboer 2002; Jähnig *et al.* 2010; Palmer *et al.* 2014). They also harbour many, increasingly endangered species that are sensitive to dispersal limitation (Ozinga *et al.* 2009; Brederveld *et al.* 2011; Wubs *et al.* 2016).

Riparian plant species may be dispersed by several vectors, including wind (anemochory), animals (zoochory), and water (hydrochory) (Soons 2006; Nilsson *et al.* 2010; Soomers *et al.* 2013). Hydrochory has been shown to be a dominant dispersal vector in riparian habitats, both in models (Soomers *et al.* 2013) and in the field: many seeds of many species are dispersed by water to riparian zones (Moggridge *et al.* 2009). In addition, hydrochory may occur over long distances: up to 152.5 km has been reported for seed mimics (Andersson *et al.* 2000). Hydrochory has been shown to bring new species into existing vegetation (Gurnell *et al.* 2008) and to be important for colonization of newly created river banks (Gurnell *et al.* 2006; Chapter 4). Yet, recent studies also reported serious constraints in the (re-)colonization of restored riparian zones (Brederveld *et al.* 2011) and in hydrochorous dispersal due to ongoing habitat fragmentation, loss of connectivity by damming (longitudinal connectivity), channelization (lateral connectivity) and flow regulation (Ozinga *et al.* 2009; Nilsson *et al.* 2010; Baattrup-Pedersen *et al.* 2013; Lorenz & Feld 2013).

Seed dispersal via hydrochory is influenced by extrinsic factors (e.g., stream discharge patterns, flow velocity, water levels and channel roughness) and intrinsic factors (e.g., seed buoyancy, seed shape and timing of seed release; Nilsson *et al.* 2010). Besides determining longitudinal dispersal distance, these factors also determine the position on the stream bank where seeds become deposited. For example, non-buoyant

seeds are likely to sink to the stream bed, but may be propelled to the floodplain by currents during high flows (Gurnell *et al.* 2007) and subsequently become spatially sorted by different seed settling velocities in analogy to the deposition of mineral sediments (Dietrich 1982; Poulsen *et al.* 2014). Buoyant seeds, on the other hand, are likely to be spread out across riparian zones following fluctuating water levels (Merritt & Wohl 2002; Van Leeuwen *et al.* 2014), where they may be concentrated when water levels are stable, or when water levels peak (visible as drift piles that mark high water lines; Nilsson & Grelsson 1990; Vogt *et al.* 2006). The eventual position along the riparian gradient has important consequences for the fate of deposited seeds, as hydrological gradients represent a strong environmental filter on recruitment (Chapter 3), and resulting vegetation patterns and diversity (Chapter 4; Andersson *et al.* 2000)

As the qualitative (suitability of deposition site) aspects of hydrochorous dispersal are at least as relevant as the more often studied quantitative aspects (distance), closer inspection of the elevational patterns of seed deposition in relation to seed and species traits may reveal important mechanisms regulating (re-)colonization. Field studies that relate seed traits to elevational patterns of deposition along riparian zones are limited and existing (Nilsson *et al.* 1991; Goodson *et al.* 2003; Gurnell *et al.* 2008; Riis *et al.* 2014) were mostly carried out in developed plant communities, in which direct seed fall from standing vegetation is likely to dominate deposition patterns. Newly created riparian zones, which are cleared of vegetation, provide an ideal environment for collecting information on hydrochorous seed deposition along riparian gradients and its consequences for (re-)colonization and potential restoration success.

We monitored year-round seed deposition in relation to water levels of newly created riparian zones to 1) assess the relative importance of hydrochory in comparison to non-hydrochorous seed delivery to restored riparian zones, 2) improve mechanistic understanding of elevational patterns of seed deposition along riparian gradients and 3) disentangle the effects of seasonality on 1 & 2. To this purpose, we monitored the natural seed rain along riparian gradients of lowland streams that had recently been excavated to bare substrate in the context of a restoration programme. By placing seed traps along a complete range of hydrological conditions (from permanently flooded to never flooded) we could compare hydrochorous dispersal to non-hydrochorous dispersal, and study the effect of hydrochory on elevational seed deposition patterns along riparian gradients.

MATERIAL AND METHODS

Study system

Stream riparian zones form the boundary between terrestrial and aquatic ecosystems. They are highly heterogeneous and dynamic, characterized by sharp environmental gradients and natural disturbance regimes by flooding (Naiman *et al.* 1993; Naiman & Décamps 1997). Their natural connectivity is high, following propagule transport by anemochory, zoochory and particularly hydrochory, one of the prerequisites for the commonly observed high biodiversity along stream riparian zones. Lowland streams differ from other stream types by their more gentle slope (0-5‰) and low flow velocities (0.05-0.6 m s⁻¹), with discharge patterns and associated flooding of riparian zones closely connected to precipitation patterns (Verdonschot & Nijboer 2002). In the Netherlands, lowland streams occur directly upstream of the Rhine-Meuse delta, on soils dominantly consisting of sand (Aeolian sand deposits) (De Vries 1976). Most streams in the Netherlands have been degraded by channelization in the last century. The associated disappearance of riparian wetlands has caused severe fragmentation of their remnants. To counteract species and habitat loss, an increasing number of restoration projects has been carried out in the past decades.

We studied three lowland streams in the Netherlands: the Hagemolenbeek (HM), Hooge Raam (HR) and Kleine Aa (KA) (52°13'0.33" N, 6°43'16.88" E; 51°42'57.65" N, 5°42'9.25" E; and 51°35'39.92" N, 5°16'38.71" E respectively). All streams had been subject to restoration measures along 0.8-2 km stream length between 2009 and 2011. Restoration involved the creation of a new channel with a raised stream bed, a narrowed channel and excavated and widened riparian zones with more gradual lateral slopes than in the old situation. All pre-existing vegetation was removed upon construction. At HM only, the riparian zone was sown with seeds of *Lolium perenne*, *Trifolium repens*, and *Phleum pratense* subsp. *pratense* (all species nomenclature following van der Meijden 2005) to minimize erosion quickly after restoration. Details on the research locations are available in Appendix A3.1 (Chapter 3).

Field methods

Natural seed rain was monitored using seed traps made by 25 x 25 cm artificial turf mats (Astroturf, with 1.5 cm bristles and ca. 8 bristles per cm²; cf. Goodson *et al.* 2003). To study seed rain along the entire hydrological gradient, three replicate transects of five seed traps were pinned to the ground perpendicular to the stream channel (Fig. 2.1). Distances between seed traps were approximately 0.5, 1.0, 3.0 and 5.0 m (from low to high elevation), and transects were 20-25 m apart, which was the maximum possible in the available area. Seed traps were placed in the field immediately after restoration (HM: December 2010, HR: May 2011 and KA: October 2011) and replaced

by new seed traps in April and October in the first year (HR and KA) or first 1.5 year (HM) after restoration to analyse seasonal differences in seed deposition. To be able to exclude seed rain of species that established in a transect during a period of seed rain monitoring we registered vegetation development (species percent cover) in permanent quadrants (25 x 50 cm) adjacent to each seed trap in July/August each year. Stream water levels were registered hourly (Fig. 2.2) using pressure transducers (Schlumberger Water Services, Delft, the Netherlands; Keller Meettechniek B.V., Reeuwijk, the Netherlands) in water level gauges within 30 m of the nearest transect. To analyse elevational patterns of seed deposition along the riparian gradient, seed deposition was related to seed trap elevation relative to the mean water level during seed rain monitoring. The relative elevation to mean water level has previously been used as a useful surrogate for otherwise strongly inter-correlated hydrological variables including flooding frequency, flooding duration and mean flooding depth (Goodson *et al.* 2003).



Figure 2.1. Field study design. To monitor seed rain along the entire hydrological gradient, three replicate transects of five seed traps (squares picture left; close-up picture right) were pinned to the ground perpendicular to the stream channel. Vegetation surveys were carried out in permanent quadrants adjacent to each seed trap (rectangles; picture left). Stream water levels were registered using pressure transducers in water level gauges within 30 m of the nearest transect.

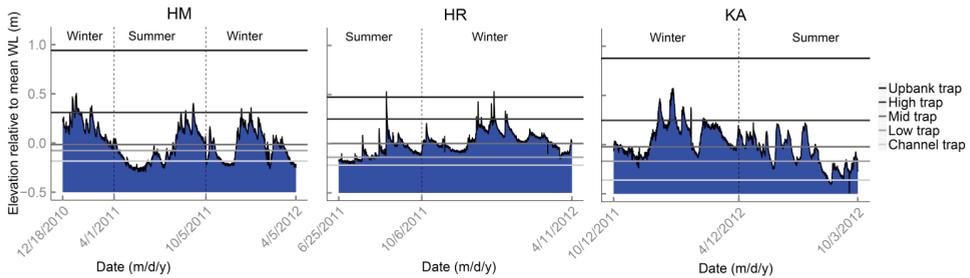


Figure 2.2. Water level fluctuations relative to the mean water level during the sampling periods for the Haggmolenbeek (HM), Hooie Raam (HR) and Kleine Aa (KA), with sampling periods separated by vertical dotted lines, and seed trap elevation (relative to mean water level) of representative transects indicated by horizontal lines.

Lab methods

After each trapping period, seed traps were taken to the laboratory and stored in plastic bags at 4°C in the dark before processing. Processing involved the extraction of deposited material by flushing the seed traps with water, followed by wet-sieving the deposits with three sieves of 2.0, 0.5 and 0.1 mm in order to remove fine silt and clay and group seeds of similar size together. In the next step, deposited material of the Haggmolenbeek seed traps was dried at 70°C for 48 hours, after which seeds were extracted by hand and identified to species level using dissecting microscopes and a seed identification guide (Cappers *et al.* 2006). This method was very time-consuming and therefore, seedling emergence trials were used to count and identify seeds in the seed traps of the remaining sites (*cf.* Boedeltje *et al.* 2002; Gurnell *et al.* 2006, 2008). This procedure involved spreading out the wet-sieved deposited material over waterlogged sand-filled trays (60 x 40 x 10 cm) in a greenhouse facility with a 15:9 h light:dark period (maintained by 400W overhead plant growth lights) and an air temperature between 15 and 25°C (*cf.* Boedeltje *et al.* 2002). To provide favourable germination conditions for as many species as possible, the trays remained waterlogged in the first 10 weeks, were slowly dried out in the following 4 weeks, and were then submerged by a 5-cm water layer for 4 weeks. Emerging seedlings were removed weekly against overcrowding and were identified to species level according to van der Meijden (2005). Although the different seed count methodologies resulted in similar amounts of species, the number of seeds was clearly higher when performing physical extraction. This difference was however largely caused by seeds of only three highly abundant species, likely indicating differences between research locations rather than differences between seed count methods (Table 2.1). Overall, this gave us no reason to expect that the different methods used affected the study results.

Plant and seed traits

To identify the type of species transported through hydrochory, and the mechanisms that shape patterns of seed deposition along riparian gradients, we analysed plant and seed traits related to hydrochory and/or expected to influence elevational patterns of seed deposition, retrieved from the LEDA trait database (Knevel *et al.* 2003; Kleyer *et al.* 2008). These included 1) species' reliance on hydrochorous dispersal (proportion of hydrochory in all assigned dispersal modes of a species, choosing from hydrochory, anemochory, zoochory, autochory, hemerochory (dispersal by man), and 'other' (tumbleweeds and raindrop-ballists)), 2) seed buoyancy (percentage of seeds still floating after 1 week in water) and 3) seed specific weight (seed mass divided by volume, assuming an ellipsoid seed shape with volume = $\frac{4}{3} \times \pi \times 0.5l \times 0.5w \times 0.5h$ for all seed species), an important determinant of settling velocity in the water column (Dietrich 1982). To identify potential consequences of seed deposition patterns for vegetation development we analysed species moisture requirements as indicated by Ellenberg F-values (Ellenberg 1988, adjusted by Hill *et al.* 1999), which have been demonstrated to be strong predictors for recruitment patterns along hydrological gradients (Chapter 3).

Data analysis

To analyse seed deposition patterns excluding direct fall from standing vegetation, we excluded from our seed trap data any seeds of species that already became established in a transect in the period of seed rain monitoring. To evaluate the importance of hydrochory relative to non-hydrochorous seed dispersal we compared seed deposition in flooded versus non-flooded seed traps during the monitoring period. In this analysis only data of the HM and KA sites were used (there were no non-flooded seed traps at the HR-site). To analyse spatial patterns in seed deposition along the riparian gradient we related seed trap position (elevation relative to the mean stream water level) to seed deposition. Analysis of seed deposition included the number of species, number of seeds, community-weighted trait means (abundance weighting as recommended for species-poor habitats like several seed traps in our dataset; Dieckmann 1995; Ellenberg 1992 in Dieckmann 2003) and community composition.

For analysing the number of species and number of seeds we used generalized linear mixed models with a negative binomial error distribution (R package lme4; Bates *et al.* 2014). For analysing community-weighted trait means we used linear mixed models and the same R package (with log- or arcsine-transformation of response values to improve normality when necessary, based on the Shapiro-Wilcoxon test). Transects and time of monitoring after restoration (either the first, second, or – only for HM – third half year after restoration) were used as random effects (intercept) in all models. The effect of season, and either flooding (categorical variable: flooded or non-

flooded) or seed trap position along the riparian gradient were added as fixed effects. In the models which tested the effect of flooding (on the HM and KA data), time of monitoring was not included as a random effect, as this interfered with the fixed effect of season. Although transects were nested within stream in the study design, streams were not included as an additional random effect. Exploratory analysis revealed that transects captured most variability of the mixed design while obtaining comparable but more stable results. Forward selections were carried out to test significance of fixed effects, with model fits determined by the Akaike's Information Criterion (AIC). In each forward selection step, a fixed effect yielding the lowest AIC was selected, with at least 2 units decrease in AIC for addition of a fixed effect (Burnham & Anderson 2002). Community composition was analysed using a partial redundancy analysis on hellinger-transformed species data (Legendre & Gallagher 2001), using the R-package *vegan* (Oksanen *et al.* 2015). Hellinger transformation was used to reduce the weight of the most abundant species (Borcard *et al.* 2011). Transects were partialled out in all multivariate analyses.

RESULTS

We retrieved 100 of the 105 seed traps that were placed in the field. Of these traps, 82 experienced flooding during the period of seed rain monitoring and 18 – only from the HM and KA sites – did not (Fig. 2.2; Table 2.1). Initial seed arrival (seed rain of species that were not yet established in a transect during seed rain monitoring; see Data analysis) was detected for 110 species and 18,842 seeds in total, of which 102 species and 17,816 seeds were deposited in flooded seed traps and 48 species in non-flooded seed traps (1,026 seeds). Although the number of species was generally comparable between sites, the overall numbers of seeds were higher at the HM site. This was largely due to three highly abundant species: *Rorippa palustris* (7,000 seeds), *Gnaphalium uliginosum* (3,028 seeds) and *Betula pendula/pubescens* (2,458 seeds), together accounting for 12,486 deposited seeds. A complete species list is given in Appendix A2.1.

Table 2.1. Overview of the number of species and number of seeds deposited in seed traps per research site, period of monitoring and season. Numbers of traps, species (Sp) and seeds are given for flooded (FL), not-flooded (Not FL) and all (TOT) monitored seed traps.

Site	Period	Season	Traps FL/ NotFL (#/#)	Sp TOT (#)	Sp FL (#)	Sp NotFL (#)	Seeds TOT (#)	Seeds FL (#)	Seeds NotFL (#)
HM	1	Winter	12/3	26	23	13	8921	8849	72
HM	2	Summer	12/3	22	21	8	3348	3181	167
HM	3	Winter	11/4	69	64	23	3804	3663	141
HR	1	Summer	15/0	27	27	-	380	380	-
HR	2	Winter	15/0	33	33	-	551	551	-
KA	1	Winter	7/3	31	28	15	1080	777	303
KA	2	Summer	10/5	27	16	20	758	415	343
All seed traps			82/18	110	102	48	18842	17816	1026

Relative importance of hydrochory for seed arrival

Hydrochory greatly contributed to seed arrival at the restored riparian zones. Average numbers of species and seeds were significantly higher in flooded seed traps than in non-flooded seed traps (Fig. 2.3 left panels; Table 2.2). For the number of species, this difference was greatly due to the fact that many species arrived exclusively at flooded seed traps (48 species, contributing 1,216 seeds). For the number of seeds, the difference was mostly generated by species that arrived both in flooded and in non-flooded traps (38 species, contributing 16,674 seeds). Of this latter group, 13 species arrived in much higher numbers at flooded seed traps than at non-flooded seed traps (14,427 versus 159 seeds; see Appendix A2.2).

These differences in seed deposition between flooded and non-flooded sites shaped differences in the arriving seed communities along the riparian gradient. Multivariate analysis showed that both flooding and season had a significant effect on seed community composition (total adjusted explained variance for HM site: $R^2 = 0.19$, $p = 0.001$, and for KA-site: $R^2 = 0.16$, $p = 0.001$; Appendix A2.3). Community-weighted trait means further showed that seeds deposited in flooded seed traps had a significantly higher reliance on hydrochory, higher seed buoyancy, lower seed specific weight and higher Ellenberg F-values than seeds deposited in non-flooded seed traps (Fig. 2.4 left panels; Table 2.2).

Apart from flooding, season of arrival explained additional variance. In winter significantly more species and seeds were deposited, with higher community weighted means for buoyancy than in summer (Figs. 2.3, 2.4; Table 2.2).

Table 2.2. Forward selections of fixed effects in (negative binomial G)LMMs explaining species number and number of seeds by the categorical variables flooding ('FL'; flooded versus non-flooded) and season ('Seas'; summer versus winter) above the dashed line, and by the variables Elevation relative to mean water level ('Elev'; exponential or quadratic when significantly better than linear, indicated in superscript with 'E' and 'Q') and season below the dashed line. Explained variance (R^2 , determined from models with a Poisson error distribution) and model fits (AIC) are given for each model. Best models, with at least 2 units AIC decrease for addition of a variable, are underlined.

# Species		# Seeds		Reliance hydr		Buoyancy		Specific weight		Ellenberg F		
Flooded versus non-flooded												
Effects	R^2	AIC	R^2	AIC	R^2	AIC	R^2	AIC	R^2	AIC	R^2	AIC
None	0	434.2	0	895.0	0	-174.0	0	56.2	0	138.7	0	220.1
Seas	0.35	417.1	0.15	890.9	0.02	-173.8	0.11	50.3	0.02	139.3	0	222.1
FL	0.11	432.0	0.44	885.5	<u>0.14</u>	<u>-182.4</u>	0.20	42.7	<u>0.06</u>	<u>136.6</u>	<u>0.18</u>	<u>208.4</u>
Seas + FL	<u>0.44</u>	<u>413.6</u>	<u>0.56</u>	<u>882.8</u>	0.16	-182.2	<u>0.30</u>	<u>34.6</u>	0.08	136.9	0.18	210.4
Seas + FL + Seas:FL	0.42	414.5	0.52	881.6	0.15	-180.3	0.30	36.1	0.08	138.8	0.19	210.7

Seed trap elevation (all traps)												
Effects	R^2	AIC	R^2	AIC	R^2	AIC	R^2	AIC	R^2	AIC	R^2	AIC
None	0	574.8	0	1179.6	0	-266.1	0	73.7	0	188.3	0	327.9
Seas	0.23	558.6	0.07	1175.4	0.02	-265.9	0.08	67.2	0.04	186.1	0.03	327.7
Elev	0.08	569.2	0.15	1176.2	<u>0.19</u>	<u>-291.4^E</u>	0.12	59.0	0.11	180.8 ^Q	0.22	303.9
<u>Seas + Elev</u>	<u>0.28</u>	<u>551.2</u>	<u>0.21</u>	<u>1171.8</u>	0.20	-292.5 ^E	<u>0.18</u>	<u>49.0</u>	<u>0.45</u>	<u>178.4^Q</u>	0.24	302.0
Seas + Elev + Seas:Elev	0.28	553.1	0.23	1172.0	0.20	-290.6 ^E	0.18	51.0	0.14	182.2 ^Q	<u>0.30</u>	<u>293.8^E</u>
Seed trap elevation (only flooded traps)												
Effects	R^2	AIC	R^2	AIC	R^2	AIC	R^2	AIC	R^2	AIC	R^2	AIC
None	0	474.0	0	975.9	0	-216.2	0	49.1	0	159.2	0	260.0
Season	0.21	456.8	0.07	969.9	0.02	-216.5	0.07	41.8	0.05	156.4	0.03	259.9
Elev	0.02	472.0 ^Q	0.19	966.9 ^Q	0.12	-227.8	0.04	46.6	0.17	146.8 ^Q	0.13	249.4
Seas + Elev	0.23	453.2 ^Q	<u>0.25</u>	<u>957.3^Q</u>	0.14	-228.8	<u>0.11</u>	<u>38.4</u>	0.22	142.9 ^Q	0.15	248.7
Seas + Elev + Seas:Elev	<u>0.38</u>	<u>447.2^Q</u>	0.43	956.7 ^Q	<u>0.18</u>	<u>-231.0^Q</u>	0.11	40.3	<u>0.28</u>	<u>137.8^Q</u>	<u>0.21</u>	<u>244.1</u>

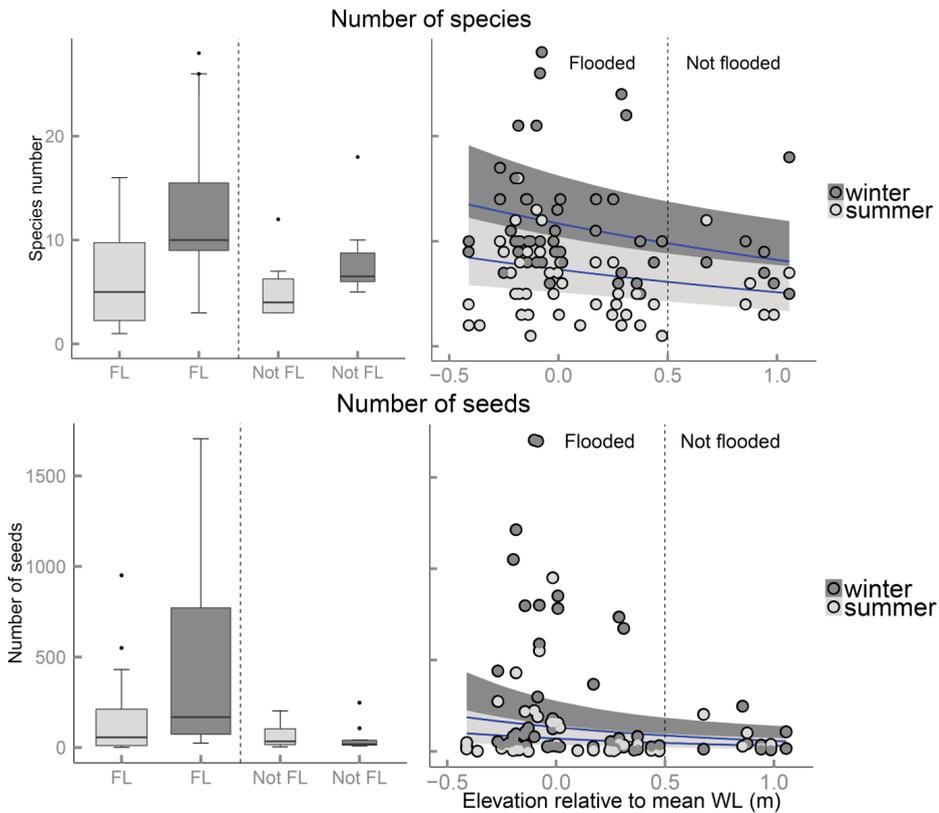


Figure 2.3. The effects of flooding and season on the number of species of deposited seeds (upper panels) and number of seeds (lower panels). A comparison of flooded (FL) and non-flooded seed traps (Not FL) is given in the left panels (box widths proportional to number of seed traps). The effect of seed trap elevation relative to mean water level is given in the right panels (negative values represent seed traps below the average water level, positive values represent seed traps above it). Summer and winter data are displayed in different greyscales. In the right panels, blue lines represent modeled relationships between field data (circles) and the explanatory variables season and elevation, as analysed in negative binomial GLMMs. Grey ribbons indicate the 95% confidence intervals (based on fixed effects only).

Elevational patterns of seed deposition along riparian gradients

Besides differences between flooded and non-flooded seed traps, more gradual patterns in seed deposition were observed along the riparian gradients. The number of seeds and species showed significant gradual decreases from the channel to the upland (Fig. 2.3; right panels). Although both response values showed signs of a peak near the average water level (i.e. zero elevation relative to mean WL), a quadratic term

for seed trap elevation (describing a unimodal pattern along the gradient) was not significantly better than the main linear term when analysing the full data-set. When we excluded the non-flooded seed traps, however, unimodal curves with peaks around the average water level gave the best fit (Appendix A2.4).

Community composition of the arriving seeds also showed a clear pattern along the riparian gradient. Multivariate analyses distinctly separated communities from different elevations along the riparian gradient (Fig. 2.5). In these analyses, both seed trap elevation and season were significant explanatory variables (total adjusted explained variation $R^2 = 20.4, 9.8,$ and 16.8 for HM, HR and KA respectively, with $p = 0.001$ for all three analyses; Appendix A2.3.1). This result was also found when only the subset of flooded seed traps was analysed, except for the KA-site where only the effect of season remained significant (Appendix A2.3.2).

Further analysis of the deposited seed communities revealed gradual decreases in community-weighted trait means from the channel to the upland for reliance on hydrochory, seed buoyancy and Ellenberg F-value (Fig. 2.4; right panels). For seed specific weight, however, a U-shaped quadratic relation was found (Fig. 2.4). When excluding the non-flooded seed traps, all relations remained more or less similar (Table 2.2; Appendix A2.4), except that seasonal differences were stronger.

Season explained additional variance in nearly all analyses on community patterns along the riparian gradient, with and without non-flooded seed traps in the analyses. In winter a larger number of seeds and species, and higher values for seed buoyancy and seed specific weight were found than in summer. Moreover, in winter higher Ellenberg F-values were observed particularly for seed communities on higher elevations in the floodplain, as visible by a significant interaction between season and Ellenberg F-value (Fig. 2.4; Table 2.2). When excluding the non-flooded seed traps, more interactions with season were significant. Particularly, in winter the deposition of seeds and species around the average waterline was less pronounced than for the strongly unimodal curves for summer (Appendix A2.4).

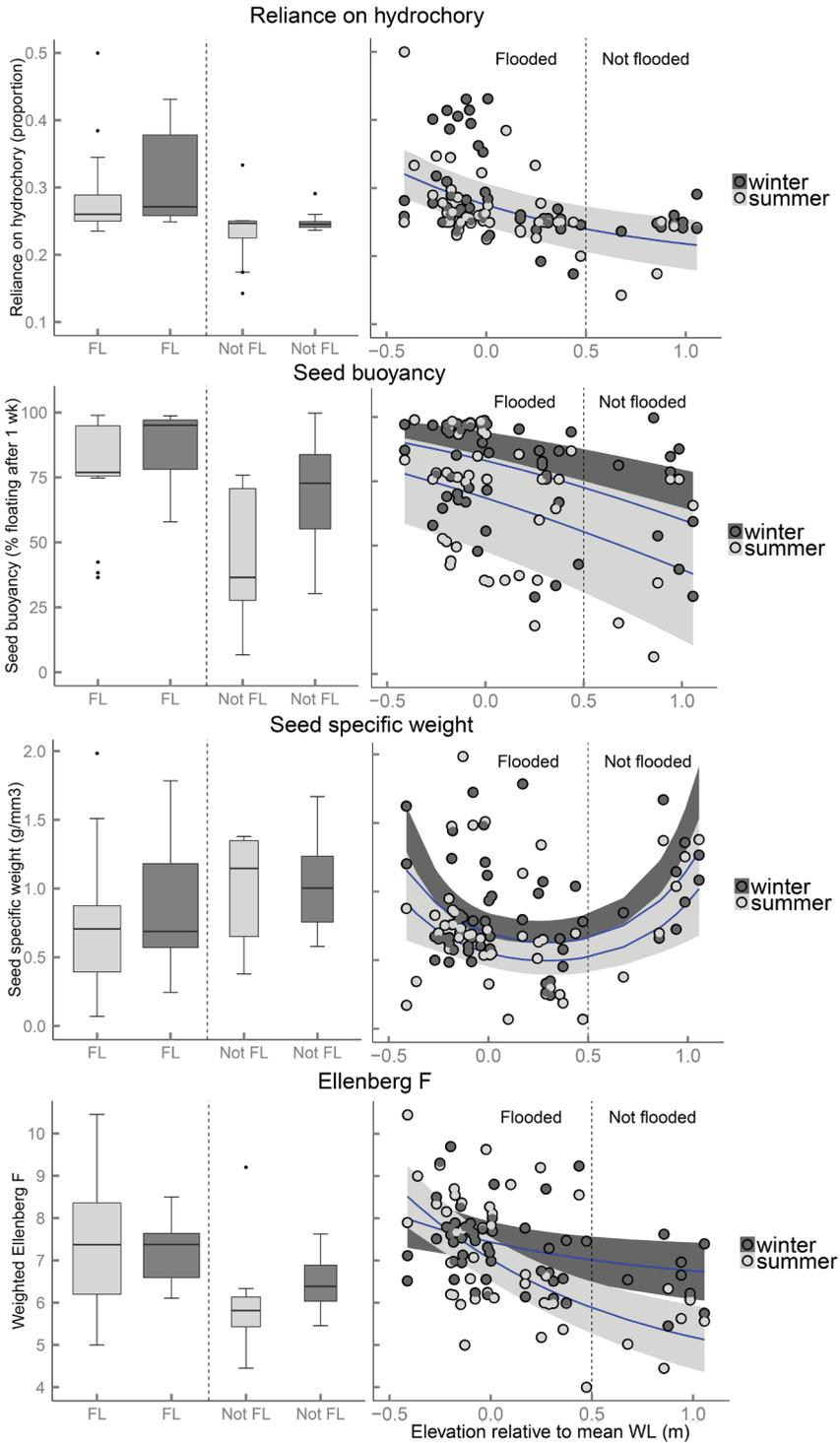


Figure 2.4. The effects of flooding and season on community-weighted means of seed traits of the deposited seed community, i.e. reliance on hydrochory, seed buoyancy, seed specific weight and Ellenberg F-value. A comparison of flooded (FL) and non-flooded (Not FL) seed traps is given in the left panels (box widths proportional to number of seed traps). The effect of seed trap elevation relative to the mean water level is given in the right panels (negative values represent seed traps below the average water level, positive values represent seed traps above it). Summer and winter data are displayed in different greyscales. In the right panels, blue lines represent modeled relationships between field data (circles) and the explanatory variables season and elevation, as analysed in LMMs. Grey ribbons indicate the 95% confidence intervals (based on fixed effects only).

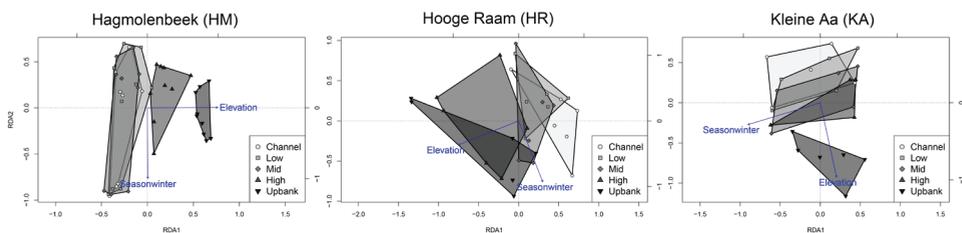


Figure 2.5. Distance triplots of partial redundancy analyses on Hellinger-transformed seed deposition per research location with respect to the explanatory variables season and seed trap elevation. Site scores are indicated by symbols, with symbol type determined by seed trap position along the riparian gradient, ranging from the dry end (upbank) to the wet end (channel) of the riparian gradient. Contour lines are added around sites scores with the same symbol type.

DISCUSSION

Relative importance of hydrochory for seed arrival

Seed deposition following transport by stream water played a very important role in seed arrival at restored lowland stream riparian zones. Both the number of seeds and the number of species were significantly higher in seed traps that were at some point flooded by stream surface water than in non-flooded seed traps. This difference was also reported in studies on seed dispersal across vegetated stream riparian zones (Goodson *et al.* 2003; Gurnell *et al.* 2008; Moggridge *et al.* 2009) and can be explained by the additive role of hydrochory to other dominant dispersal processes such as anemochory and zoochory. In our study, 48 species were deposited exclusively, and many of the abundant species were deposited dominantly, at flooded seed traps. In accordance with studies on vegetated riparian zones, the effect of hydrochory was particularly strong in winter, delivering higher numbers of seeds and species than in summer (Gurnell *et al.* 2008; Moggridge *et al.* 2009).

The community composition of seeds that arrived in flooded seed traps differed from that in non-flooded seed traps, which was also clearly visible in the

analysed species traits. Species arriving in flooded seed traps were more typically water-dispersers (more reliant on hydrochory), had a higher seed buoyancy and a lower seed specific weight than species arriving in non-flooded seed traps. Such traits are typical for riparian plant species: Johansson *et al.* (1996) found that riparian species along rivers had significantly higher seed buoyancies than species from other ecosystem types. Also, the species arriving in flooded seed traps were characteristic of habitats with higher moisture levels (as indicated by their higher Ellenberg F-values), as riparian plant species would be expected to be. One explanation for the large amounts of riparian plant species in the flooded seed traps is the direct vicinity of riparian plant populations to streams, providing ample seed sources. Seeds of these species become dropped directly in the water or on floodplains where they will easily be carried away by surface water during high flows (Nilsson *et al.* 2010). For the same reason aquatic species might be expected to contribute substantially to hydrochorous propagule pools, but in our study the number of seeds of this species group was low compared to riparian species, probably because of the dominantly vegetative regeneration strategies of aquatic species (Barrat-Segretain 1996; Boedeltje *et al.* 2003). A second explanation for the large amounts of riparian plant species in the flooded seed traps might be that riparian plants produce long-floating seeds, which are ideally suited to be deposited by the stream water at the shorelines where they prefer to germinate and grow (Chapter 4): a form of highly effective 'directed dispersal' (Seiwa *et al.* 2008; M.B. Soons *et al.*, unpublished data).

Despite the high contribution of riparian plants in the flooded traps, a large amount of variation was evident for all seed traits and also many non-typical water-dispersers arrived via hydrochory. This may in part be explained by the regular occurrence of other species than typical riparian plant species in floodplains (e.g., common and/or opportunistic terrestrial species; van Eck *et al.* 2004), of which seeds also easily become part of the hydrochorous seed pool. Additionally, at unrestored stream sections the upland is very close to the stream, which facilitates seeds of upland species to end up in the stream via wind, animals or overland flow after heavy rains (Vittoz & Engler 2007). Otherwise, typically wind-dispersed species may travel long distances (Soons *et al.* 2004; Soons 2006) before being 'trapped' in a stream (Nilsson *et al.* 2010). These seeds often float well, resulting in 'non-standard' hydrochorous dispersal that may incidentally be effective (Higgins *et al.* 2003; Merritt & Wohl 2006; Nathan *et al.* 2008).

Elevational patterns of seed deposition along riparian gradients and explanatory mechanisms

The numbers of seeds and species both decreased along the channel-upland gradient. This suggests that the number of hydrochorously-dispersed seeds decreases with

increasing elevation, which was supported by gradual declines in community-weighted means for reliance on hydrochory, seed buoyancy and Ellenberg F-value along the gradient (i.e., seeds becoming less similar to the hydrochorous seed pool with increasing elevation). Within the hydrochorously-deposited seeds, however, also patterns in seed deposition along the riparian gradient occurred. Firstly, the number of seeds and species both showed a peak around the average water line (additionally to the gradual decrease), probably by the deposition of high numbers of floating seeds. Floating seeds may be entrapped in riparian vegetation (Chambert & James 2009), or get stranded by retreating water levels (Merritt & Wohl 2002), which frequently occurs along the average water line. Particularly species with long-floating seeds are known to get dominantly deposited around this fluctuating water line (Nilsson *et al.* 2002), or at higher elevations in drift lines (Vogt *et al.* 2006, 2007). Unfortunately, the quality of the buoyancy data does not allow us to detect patterns in the deposition of long-floating seeds; the data represent floating percentages after only one week in water, which are not sufficiently representative for long floating times (months, years). Reliance on hydrochory, however, did show a peak around the average water line (in winter), indicating that seeds arriving around the average water line were typical water-dispersers.

Secondly, community-weighted means for seed specific weight increased towards the wet end of the gradient, opposite of what would be expected given the difference in seed specific weight between hydrochorous and non-hydrochorous seeds. Apparently, hydrochorous seeds with a higher specific weight became mainly deposited at lower elevations, while hydrochorous seeds with a lower specific weight became deposited at higher elevations within the flooded range. This pattern resembles spatial sorting in the deposition of non-floating particles. Mineral sediments with different settling velocities (Dietrich 1982) have been shown to become deposited at different distances from the stream during flooding (Poulsen *et al.* 2014). In analogy to this, non-buoyant seeds with high specific weights may become deposited close to the channel, while non-buoyant seeds with lower specific weights end up at further distances (elevations) from the stream. Gurnell (2007) and Chambert & James (2009) proposed such analogies between the deposition of seeds and that of mineral sediments. Our data supports this and suggests an important role for seed specific weight in hydrochorous seed sorting across the riparian zone.

Lastly, community-weighted Ellenberg F-values indicated that species with adult optima at wetter conditions dominated seed arrival at lower elevations (channel seed traps), while species with drier optima dominated at higher elevations in the floodplain. This species sorting was stronger than would be expected by a gradual decrease in hydrochorous seeds, indicating that hydrochory brings many seeds to their preferred microhabitats. As mentioned above, seed buoyancy was probably

important to this form of directed dispersal, stimulating seeds with a high buoyancy to be deposited around the average water line or higher, while for seeds with a low buoyancy deposition under water is stimulated (Coops & Van der Velde 1995; Boedeltje *et al.* 2004). Although our study does not allow to compare the relative contributions of the mechanisms that shape seed deposition patterns, it clearly indicates that seed buoyancy, seed specific weight and stream surface water (flow and level) in combination are likely to result in seed deposition and species sorting across the riparian zone.

Seasonal differences

Our data shows that seed arrival is higher in winter than in summer, while comparable numbers or even the opposite has been found in existing vegetation where direct fall from standing vegetation may contribute largely to seed deposition (Moggridge *et al.* 2009; A.G. Garssen, unpublished data). Specifically for hydrochorous dispersal, the most important effect of seasonality is that in winter, more seeds of more species are dispersed, supporting earlier studies (Gurnell *et al.* 2008; Moggridge *et al.* 2009), and that wetland species are more widely distributed over the riparian zone (as indicated by the community-weighted Ellenberg F-values). This underlines the importance of high flows during winter, enabling riparian plant species to colonize a wider range of elevations across riparian zones.

Consequences of hydrochorous seed dispersal for vegetation development

Our results demonstrate that hydrochory contributes importantly to the arrival of seeds in riparian zones: hydrochorous dispersal results in the arrival of many seeds of many species in riparian zones, potentially contributing to local vegetation diversity (Andersson *et al.* 2000; Jansson *et al.* 2005) and generates a species sorting template on which further community processes may operate to generate vegetation patterns (Silvertown *et al.* 1999, 2015; Chapter 3, 4). Particularly, hydrochorous dispersal contributes to the arrival of seeds of (common) riparian wetland species, and brings many seeds to their preferred microhabitats, thereby playing an important role in their population dynamics and colonization potential (Brederveld *et al.* 2011; Wubs *et al.* 2016). Hydrochorous dispersal may further contribute to the dispersal of non-typical riparian species of which many are deposited in riparian zones – although not necessarily at favourable sites. In these ways, hydrochory is likely to have important consequences for riparian vegetation development, which is expected to be particularly strong at recently excavated stream riparian zones. In fully developed vegetation, on the other hand, the contribution of hydrochory to (re-)colonization and gene flow is likely to be lower, as it is more difficult for arriving seeds to germinate and establish in existing plant communities.

The above has several implications for the conservation and restoration of lowland riparian zones, particularly in human-dominated landscapes. Firstly, in increasingly human-dominated landscapes the loss of connectivity between stream sections (due to damming, diversions) and between the stream and its riparian zone (due to channelization and prevention of flooding) currently greatly reduces the potential for hydrochorous dispersal of riparian plant species (Ozinga *et al.* 2009; Nilsson *et al.* 2010). This ongoing fragmentation increasingly hampers gene flow between existing populations and re-colonization of restored sites (as also shown for mountain streams by Brederveld *et al.* 2011), and restoration of connectivity and particularly of flooding seems essential. However, seed arrival following hydrochory generally results in common riparian species and reflects the environmental quality of the catchment (Baatrup-Pedersen *et al.* 2013; Lorenz & Feld 2013), so that apart from the restoration of flooding, landscape-level conservation and restoration planning should be carried out to optimize connectivity for wanted species (e.g., Verhoeven *et al.* 2008). Secondly, to ensure a quick colonization of restored riparian zones, with a range of typical riparian plant species, restoration activities removing any unwanted existing vegetation should best be finished before winter. With such timing, restoration optimally benefits from the seed deposition of riparian species by winter floods. Finally, climatic changes resulting in changes in flooding regimes which are likely to impact riparian vegetation (Garssen *et al.* 2014, 2015), are also likely to impact riparian vegetation through changes in hydrochory. Restoration activities should therefore aim at lateral riparian profiles that allow for flooding even under projected future climatic conditions.

ACKNOWLEDGEMENTS

We thank Marwin Hofstede and the staff from the supporting water boards for their constructive collaboration. This study was supported by the water boards 'Aa en Maas', 'De Dommel' and 'Regge en Dinkel', and co-funded by Agentschap NL (Rijksdienst voor Ondernemend Nederland), the Foundation for Applied Water Research (STOWA) and personal grants to M. B. Soons (Netherlands Organization for Scientific Research, NWO-ALW Meervoud and Vidi grants).

Appendix A2.1. Overview of deposited seed species

Table A2.1.1. Total number of deposited seeds per species for the Hagmolenbeek (HM), Hooge Raam (HR) and Kleine Aa (KA) sites, separated for each trapping period (p1, p2 or p3).

Species	HM p1	HM p2	HM p3	HR p1	HR p2	KA p1	KA p2
<i>Achillea millefolium</i>	0	0	1	0	0	0	0
<i>Agrostis capillaris/canina</i>	0	178	1	0	0	0	0
<i>Alisma lanceolatum</i>	0	0	18	0	0	0	0
<i>Alisma plantago-aquatica</i>	0	236	406	24	108	0	137
<i>Allium schoenoprasum</i>	1	0	0	0	0	0	0
<i>Alnus glutinosa</i>	45	1	165	0	0	4	0
<i>Alopecurus geniculatus</i>	0	0	8	0	0	0	0
<i>Angelica sylvestris</i>	1	0	1	0	0	0	0
<i>Atriplex patula</i>	0	0	0	0	1	0	0
<i>Betula pendula/pubescens</i>	465	593	1400	0	0	0	0
<i>Betula pubescens</i>	0	0	0	6	22	29	1
<i>Bidens cernua</i>	0	0	1	0	0	0	0
<i>Bidens frondosa</i>	0	6	25	0	0	0	0
<i>Bidens tripartita</i>	0	0	13	5	6	0	6
<i>Bromus hordeaceus ssp hordeaceus</i>	0	0	1	0	0	0	0
<i>Callitriche platycarpa/obtusangula/stagnalis</i>	0	0	18	12	16	0	0
<i>Capsella bursa-pastoris</i>	42	41	2	0	0	0	0
<i>Carex oederi ssp oederi</i>	0	0	22	0	0	0	0
<i>Carex ovalis</i>	0	0	1	0	0	0	0
<i>Carex pallescens</i>	0	0	1	0	0	0	0
<i>Carex pseudocyperus/rostrata</i>	1	0	5	0	0	0	0
<i>Carex remota</i>	0	0	1	0	0	0	0
<i>Carex riparia</i>	0	0	1	0	0	0	0
<i>Carex sp</i>	0	0	1	0	0	0	0
<i>Cerastium glomeratum</i>	0	0	0	3	0	1	0
<i>Ceratophyllum demersum</i>	0	0	1	0	0	0	0
<i>Chenopodium album</i>	0	0	0	0	0	26	8
<i>Chenopodium album/polyspermum</i>	391	189	239	0	0	0	0
<i>Cirsium arvense</i>	0	0	0	1	3	0	0
<i>Conyza canadensis</i>	0	0	0	18	8	5	71
<i>Conyza sumatrensis</i>	0	3	0	0	0	0	0
<i>Digitaria ischaemum</i>	0	0	0	0	3	0	0
<i>Echinochloa crus-galli</i>	56	69	36	0	0	53	152

Table A2.1.1. continued

Species	HM p1	HM p2	HM p3	HR p1	HR p2	KA p1	KA p2
<i>Eleocharis palustris</i>	0	0	1	0	0	0	0
<i>Epilobium ciliatum</i>	0	0	0	0	0	46	0
<i>Epilobium tetragonum/ciliatum/parviflorum</i>	0	0	0	30	28	0	0
<i>Euphrasia stricta</i>	0	0	1	0	0	0	0
<i>Fagus sylvatica</i>	0	0	6	0	0	0	0
<i>Festuca brevipilla/rubra/filiformis</i>	0	0	2	0	0	0	0
<i>Festuca pratensis</i>	0	0	1	0	0	0	0
<i>Filipendula ulmaria</i>	0	0	0	0	2	0	0
<i>Galinsoga parviflora</i>	0	0	0	0	1	0	0
<i>Galinsoga quadriradiata</i>	0	0	0	0	0	2	108
<i>Glyceria fluitans</i>	1	8	12	1	0	0	1
<i>Glyceria maxima</i>	0	0	0	5	17	1	22
<i>Gnaphalium luteo-album</i>	0	0	0	5	6	0	0
<i>Gnaphalium uliginosum</i>	853	1179	581	6	10	399	0
<i>Hieracium sp*</i>	0	1	1	0	0	0	0
<i>Holcus lanatus</i>	1	0	3	0	0	0	0
<i>Holcus mollis</i>	0	0	1	0	0	0	0
<i>Hypericum sp*</i>	128	0	4	0	0	0	0
<i>Hypericum perforatum</i>	0	0	0	2	24	0	0
<i>Isolepis setacea</i>	7	10	13	0	0	1	0
<i>Jacobea sp</i>	0	0	0	2	0	0	0
<i>Leontodon autumnalis</i>	0	0	0	0	0	0	1
<i>Luzula luzuloides</i>	0	0	1	0	0	0	0
<i>Lycopus europaeus</i>	20	0	36	0	0	192	0
<i>Lythrum salicaria</i>	0	0	0	2	11	4	14
<i>Matricaria chamomilla</i>	0	0	4	0	1	1	0
<i>Matricaria discoidea</i>	0	0	0	0	0	1	0
<i>Mentha aquatica</i>	0	0	0	0	0	27	2
<i>Mentha aquatica x verticillata</i>	0	0	0	0	1	0	0
<i>Myosotis scorpioides</i>	0	0	0	3	6	1	0
<i>Nasturtium microphyllum</i>	0	0	1	0	0	0	0
<i>Oenanthe aquatica</i>	0	0	0	0	0	1	1
<i>Persicaria lapathifolia</i>	7	332	16	0	0	0	0
<i>Persicaria maculosa</i>	1	0	2	152	26	6	0
<i>Persicaria minor</i>	0	12	1	0	0	0	0
<i>Persicaria mitis</i>	0	1	2	0	0	0	0

Table A2.1.1. continued

Species	HM p1	HM p2	HM p3	HR p1	HR p2	KA p1	KA p2
<i>Phalaris arundinacea</i>	0	0	1	0	0	0	0
<i>Phragmites australis</i>	0	0	171	0	0	1	1
<i>Plantago major ssp major</i>	0	0	0	9	13	0	0
<i>Poa annua</i>	0	0	4	0	0	0	0
<i>Poa trivialis</i>	0	0	5	0	0	0	0
<i>Polygonum aviculare</i>	2	0	14	1	0	1	0
<i>Potamogeton alpinus/crispus/natans</i>	7	0	3	0	0	0	0
<i>Potentilla anserina</i>	0	0	0	0	0	1	0
<i>Potentilla sp*</i>	0	0	0	5	2	0	0
<i>Primula vulgaris</i>	0	0	0	0	1	0	1
<i>Ranunculus flammula</i>	0	4	0	0	0	0	0
<i>Ranunculus ololeucos</i>	0	0	1	0	0	0	0
<i>Ranunculus peltatus</i>	0	3	9	0	0	0	0
<i>Ranunculus repens</i>	0	0	0	0	0	1	0
<i>Ranunculus sceleratus</i>	0	148	130	71	76	118	135
<i>Rorippa palustris</i>	6861	0	0	4	8	112	15
<i>Rubus fruticosus</i>	0	0	2	0	0	0	0
<i>Rumex hydrolapathum</i>	0	0	0	0	0	0	1
<i>Rumex obtusifolius</i>	3	93	34	0	1	0	1
<i>Sagina procumbens</i>	0	0	0	3	6	0	0
<i>Salix cinerea</i>	0	0	0	0	0	0	1
<i>Salvia officinalis</i>	0	0	1	0	0	0	0
<i>Sambucus racemosa</i>	0	0	1	0	0	0	0
<i>Scirpus sylvaticus</i>	1	0	0	0	0	0	0
<i>Scrophularia auriculata/nodosa/umbrosa</i>	0	0	3	0	0	0	0
<i>Senecio vulgaris</i>	0	0	0	1	7	0	2
<i>Solanum nigrum ssp nigrum</i>	0	0	18	0	13	23	0
<i>Sonchus arvensis</i>	0	0	0	0	0	1	2
<i>Sparganium emersum</i>	2	0	24	0	0	0	0
<i>Sparganium emersum/erectum</i>	0	0	0	0	0	1	49
<i>Sparganium erectum</i>	12	0	32	0	0	0	0
<i>Spergula arvensis</i>	2	0	4	0	0	1	6
<i>Stellaria media</i>	9	7	32	6	18	13	15
<i>Tanacetum vulgare</i>	0	0	1	0	0	0	0
<i>Taraxacum officinale</i>	0	0	11	0	0	0	1
<i>Thuja plicata</i>	0	0	3	0	0	0	0
<i>Trifolium repens</i>	0	0	0	0	0	0	4
<i>Typha latifolia/Sparganium emersum/erectum</i>	0	0	0	2	104	0	0

Table A2.1.1. continued

Species	HM p1	HM p2	HM p3	HR p1	HR p2	KA p1	KA p2
<i>Urtica dioica</i>	2	0	53	0	1	7	0
<i>Valeriana officinalis</i>	0	0	1	0	0	0	0
<i>Veronica catenata</i>	0	234	189	1	1	0	0

**Hieracium* sp: *Hieracium umbellatum/laevigatum/sabaudum/vulvatum/pilosella*

**Hypericum* sp: *Hypericum elodes/humifusum/maculatum/perforatum/tetrapterum*

**Potentilla* sp: *Potentilla anglica/anserina/argentea/erecta/reptans/sterilis/tabernaemontani*

Appendix A2.2. Number of seeds per species in flooded versus non-flooded seed traps

Table A2.2.1. Overview of deposited seeds of species that arrived in both flooded and non-flooded seed traps, with the total number of seeds (subdivided in flooded (FL) and non-flooded (notFL) seed traps) and delta AIC values (dAIC) for the addition of flooding as a fixed effect to Poisson GLMMs explaining the number of seeds deposited. Significant model improvements (dAIC of -2.0 or lower; Burnham & Andersson 2002) are underlined and in bold. Transects were included as random effect (intercept) in all models. Species are ordered in three groups separated by horizontal lines, showing significantly more seeds at flooded seed traps (upper group; positive estimates), non-significantly different numbers at flooded and non-flooded seed traps (center), or significantly more seeds at non-flooded seed traps (lower group; negative estimates).

Species	Tot nr seeds	Nr seeds FL	Nr seeds notFL	dAIC	Estimate
<i>Rorippa palustris</i>	6988	6958	30	<u>-4142.1</u>	4.5
<i>Gnaphalium uliginosum</i>	3012	3000	12	<u>-1399.5</u>	4.3
<i>Betula pendula/pubescens</i>	2458	2415	43	<u>-869.3</u>	2.7
<i>Alisma plantago-aquatica</i>	779	774	5	<u>-451.9</u>	4.1
<i>Ranunculus sceleratus</i>	531	510	21	<u>-178.4</u>	2.1
<i>Alnus glutinosa</i>	215	211	4	<u>-77.9</u>	2.7
<i>Agrostis capillaris/canina</i>	179	166	13	<u>-24</u>	1.2
<i>Hypericum sp*</i>	132	121	11	<u>-14.2</u>	1.1
<i>Rumex obtusifolius</i>	131	121	10	<u>-15.1</u>	1.2
<i>Urtica dioica</i>	62	59	3	<u>-20</u>	2
<i>Epilobium ciliatum</i>	46	42	4	<u>-2.9</u>	1
<i>Betula pubescens</i>	30	28	2	<u>-4.2</u>	1.5
<i>Glyceria maxima</i>	23	22	1	<u>-6.8</u>	2.2
<i>Chenopodium album/polyspermum</i>	819	614	205	0.8	-0.1
<i>Echinochloa crus-galli</i>	366	246	120	-0.2	-0.2
<i>Capsella bursa-pastoris</i>	85	69	16	1.5	0.2
<i>Sparganium erectum</i>	44	31	13	1.1	-0.3
<i>Mentha aquatica</i>	29	16	13	1.5	-0.3
<i>Sparganium emersum</i>	26	23	3	-0.3	0.8
<i>Glyceria fluitans</i>	22	18	4	1.6	0.3
<i>Bidens tripartita</i>	19	13	6	1.1	-0.5
<i>Polygonum aviculare</i>	17	14	3	1.3	0.5
<i>Spergula arvensis</i>	13	7	6	0.1	-0.8
<i>Taraxacum officinale</i>	12	6	6	-0.7	-1
<i>Potamogeton alpinus/crispus/natans</i>	10	6	4	0.6	-0.8
<i>Persicaria maculosa</i>	9	8	1	1.4	0.8
<i>Holcus lanatus</i>	4	2	2	0.7	-1.2

table A2.2.1. continued

Species	Tot nr seeds	Nr seeds FL	Nr seeds notFL	dAIC	Estimate
<i>Sonchus arvensis</i>	3	2	1	1.8	-0.5
<i>Persicaria mitis</i>	3	2	1	1.8	-0.5
<i>Rubus fruticosus</i>	2	1	1	1.5	-1
<i>Oenanthe aquatica</i>	2	1	1	1.7	-0.8
<i>Lycopus europaeus</i>	248	89	159	<u>-157.4</u>	-1.6
<i>Galinsoga quadriradiata</i>	110	2	108	<u>-326.4</u>	-5.4
<i>Conyza canadensis</i>	76	32	44	<u>-172.2</u>	-3.9
<i>Stellaria media</i>	76	5	71	<u>-33.7</u>	-1.4
<i>Solanum nigrum ssp nigrum</i>	41	16	25	<u>-14.2</u>	-1.3
<i>Chenopodium album</i>	34	11	23	<u>-13.4</u>	-1.4
<i>Lythrum salicaria</i>	18	8	10	<u>-4.6</u>	-1.3

**Hypericum* sp: *Hypericum elodes/humifusum/maculatum/perforatum/tetrapterum*

Appendix A2.3. Multivariate analyses

Table A2.3.1. Overview of conditional effects (flooding and season) in partial redundancy analyses on the number of deposited seeds (Hellinger-transformed), separately per research location (only for the HM and KA-sites, as there were no non-flooded seed traps at the HR-site).

HM site: Variable	Explains %	F	P
Flooding	11.8	7.5	0.001
Season	6.7	4.6	0.001

KA site: Variable	Explains %	F	P
Season	12.7	4.5	0.001
Flooding	3.2	1.8	0.033

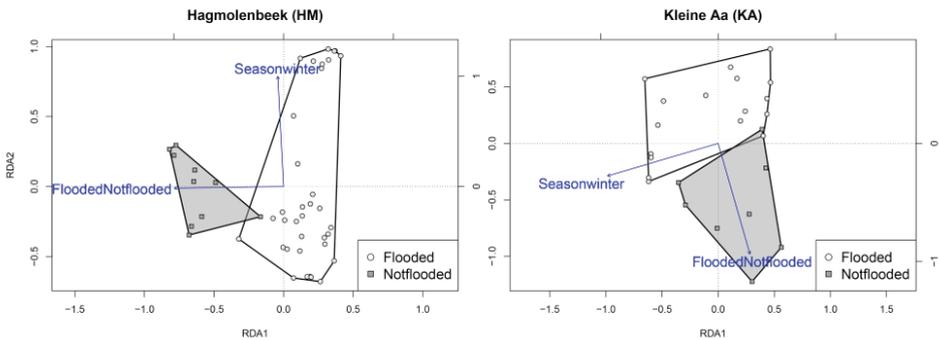


Figure A2.3.1. Distance triplots of partial redundancy analyses on Hellinger-transformed seed deposition per research location with respect to the explanatory variables season and flooding. Site scores are indicated by symbols, with different symbol type for flooded versus non-flooded seed traps. Contour lines are added around sites scores with the same symbol type.

Table A2.3.2. Overview of conditional effects (seed trap elevation and season) in partial redundancy analyses on the number of deposited seeds (Hellinger-transformed), separately per research location (HM, HR and KA-site respectively), using the combined data of flooded and non-flooded seed traps.

HM site: Variable	Explains %	F	P
Elevation	13.6	8.6	0.001
Season	6.8	4.7	0.001
HR site: Variable	Explains %	F	P
Elevation	4.9	3.0	0.001
Season	4.9	2.8	0.003
KA site: Variable	Explains %	F	P
Season	12.7	2.0	0.001
Elevation	4.1	4.6	0.022

Table A2.3.3. Overview of conditional effects (seed trap elevation and season) in partial redundancy analyses on the number of deposited seeds (Hellinger-transformed), separately per research location (HM, HR and KA-site respectively), using the data of only the flooded seed traps.

HM site: Variable	Explains %	F	P
Elevation	13.9	7.7	0.001
Season	10.2	5.7	0.002
HR site: Variable	Explains %	F	P
Elevation	4.9	3.0	0.001
Season	4.9	2.8	0.003
KA site: Variable	Explains %	F	P
Season	20.4	4.7	0.001
Elevation	-0.2	1.0	0.465

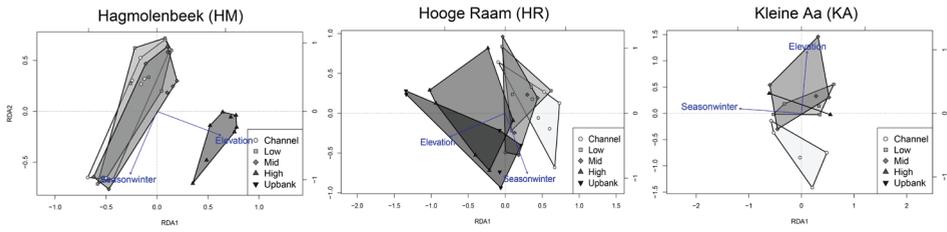


Figure A2.3.2. Distance triplots of partial redundancy analyses on Hellinger-transformed seed deposition per research location with respect to the explanatory variables season and seed trap elevation, using the subset of only the flooded seed traps. Site scores are indicated by symbols, with symbol type determined by seed trap position along the riparian gradient, ranging from the dry end (upbank) to the wet end (channel) of the riparian gradient. Contour lines are added around sites scores with the same symbol type. Upbank traps are missing in the triplots for the HM and KA-sites as these traps were not flooded.

Appendix A2.4. Seed deposition patterns within the flooded seed traps

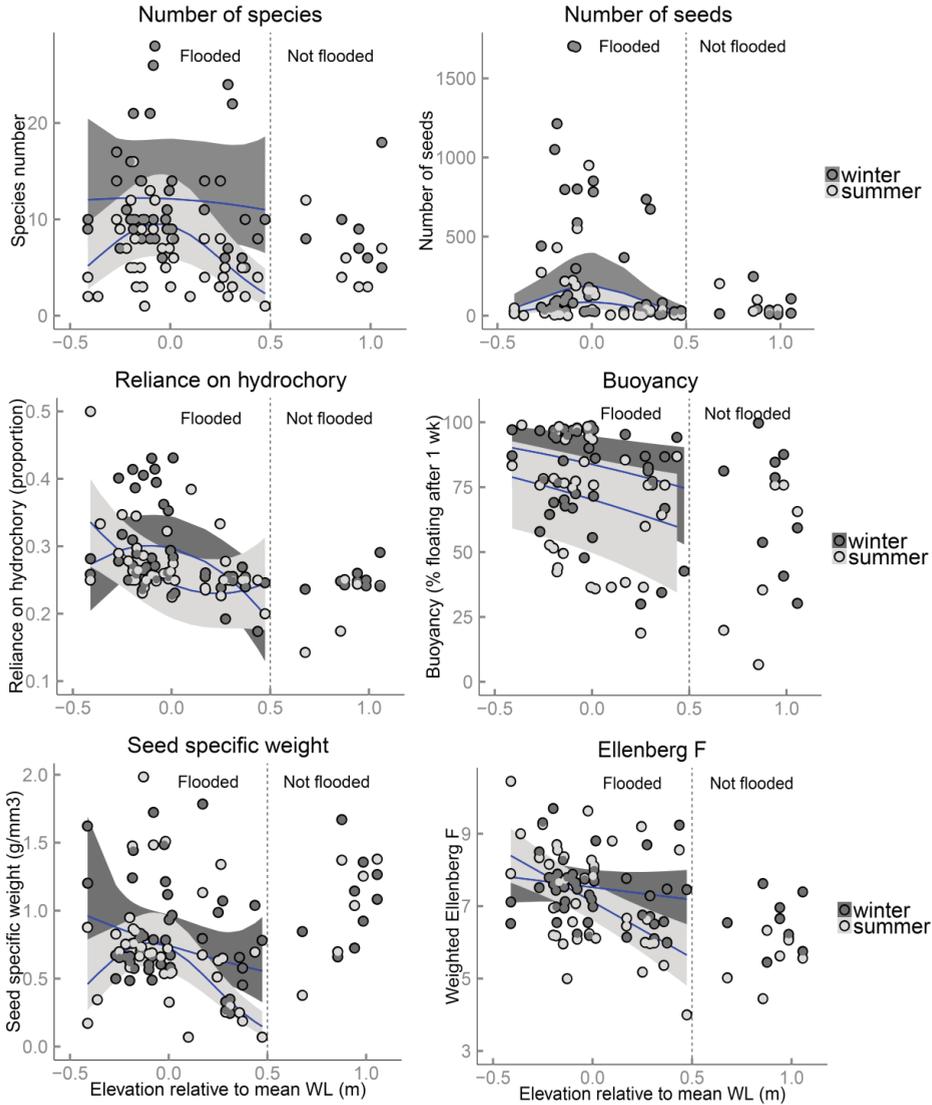


Figure A2.4.1. The effects of elevation and season on community-weighted means of seed traits of the deposited seed community, i.e. reliance on hydrochory, seed buoyancy, seed specific weight and Ellenberg F-value. The effect of seed trap elevation relative to the mean water level is given (negative values for seed traps below the average water level, and positive values for seed traps above it). Summer and winter data are displayed by different greyscales. Blue lines represent modeled relationships between the flooded field data (circles) and the explanatory variables season and elevation, as analysed in LMMs. Grey ribbons indicate the 95% confidence intervals (based on fixed effects only). Non-flooded plot data are shown as reference only.



Chapter 3

Early plant recruitment stages set the template for the development of vegetation patterns along a hydrological gradient

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ABSTRACT

Recruitment processes are critical components of a plant's life cycle. However, in comparison with later stages in the plant life cycle (e.g. competition among adults), relatively little is known about their contribution to the regulation of plant species distribution. Particularly little is known about the individual contributions of the three main recruitment processes—germination, seedling survival, and seedling growth—to community assembly, while quantitative information on these contributions is essential for a more mechanistic understanding of the regulation of plant species distribution and biodiversity.

Riparian zones along streams provide a globally-relevant case study for evaluating the importance of the different stages of plant recruitment. The natural hydrological gradients of stream riparian zones are currently being restored after a period of worldwide habitat degradation. To identify how recruitment contributes to vegetation patterns and biodiversity in riparian zones, we carried out field experiments at restored lowland streams. We quantified the germination of introduced seeds, and survival and growth of introduced seedlings of 17 riparian plant species across a gradient from the stream channel to upland.

The hydrological gradient of riparian zones acted as a strong environmental filter on all three recruitment processes, through imposing an abiotic limitation (excess water) at low elevations and a resource limitation (water shortage) at higher elevations. Other variables, such as soil organic matter content and nutrient availability, only affected recruitment marginally.

Species-specific patterns of environmental filtering initiated niche segregation along the riparian gradient during all three recruitment processes, but particularly during germination and seedling growth. These recruitment niches appeared strongly related to indicator values for adult distribution optima, suggesting that at least some riparian plant species may have evolutionary adaptations that promote recruitment under favourable hydrological conditions for adult growth and reproduction.

Our results suggest that strong environmental filtering during germination and seedling growth plays an important role in determining later adult distributions, by forming the spatial template on which all subsequent processes operate. In addition to well-known mechanisms, such as competitive exclusion at the adult stage, environmental filtering during early recruitment stages already strongly affect plant distribution and diversity.

INTRODUCTION

One of the main challenges in ecology is to understand the mechanisms regulating species distribution and biodiversity. Niche differentiation is a major concept in this field, explaining species distributions by interspecific differences in ability to gather

resources (Tilman 1982), withstand adverse conditions (Kenkel et al. 1991), or colonize empty habitats (Grubb 1977). This combination of abiotic constraints and biotic interactions forms an 'environmental filter' (sensu van der Valk 1981; Keddy 1992; ter Steege & Zagt 2002) for species establishment and persistence, which segregates species along environmental or temporal niches (Silvertown 2004). With every species occupying its own niche, stable coexistence in an ecosystem is promoted which generally increases biodiversity.

Although niche differentiation along environmental axes has been shown in many studies (Silvertown 2004), it is often unclear at which stage in a plant's life cycle such filters operate: during early stages, thereby preventing occupation of the full potential niche of adult plants (Grubb 1977; Grime 2001), or at later stages, e.g. through competitive interactions among adults (Wedin & Tilman 1993). Moreover, several early recruitment processes can be distinguished, namely germination, seedling survival, and seedling growth, and their relative contributions to niche segregation and species sorting remain unclear. While early recruitment stages are increasingly recognized as determinants of adult species distributions (Evans & Etherington 1990; Eriksson & Ehrlén 1992; Kotorová & Lepš 1999; Stampfli & Zeiter 2008), studies to date have focused either on one individual recruitment stage or on their combined result (total seedling establishment). Hence, quantitative information on the relative importance of the different stages to recruitment and adult species distributions is generally lacking. Such information would add significantly to our understanding of community assembly and biodiversity.

Recruitment stages play a particularly important role in dynamic environments, where disturbances promote species coexistence by setting back succession, creating opportunities for new establishment (Shea *et al.* 2004). Riparian zones along streams provide a typical example of such habitats, where spatial and temporal variation in flooding (abiotic limitation) and drought (resource limitation) stimulate community re-assembly and impose strong environmental filters. The natural dynamics in riparian zones coincide with a strong environmental gradient from the stream channel to uplands, providing a range of hydrological niches, which have been demonstrated to segregate species and promote species coexistence (Silvertown *et al.* 1999). The consequent vegetation patterns along riparian gradients may be induced by abiotic constraints on recruitment (Keddy & Ellis 1985; Hölzel & Otte 2003; van Eck *et al.* 2004) and adult stages (Squirres, L. & van der Valk 1992), as well as by interspecific competition among adult plants (Grace & Wetzel 1982; Kotowski *et al.* 2006). Hence, it remains difficult to evaluate how (and how much) recruitment processes, or their separate stages, contribute to the high biodiversity and commonly observed gradients found in vegetation along stream riparian zones (Naiman & Décamps 1997; Pollock *et al.* 1998; Ward 1998).

Such information would be highly relevant, as streams and their riparian zones are highly vulnerable freshwater systems. They are increasingly threatened across the world by anthropogenic modifications, such as damming, channelization, and water abstraction (Malmqvist & Rundle 2002), as well as by projected increases in climate-induced droughts (Wetherald & Manabe 2002; Milly *et al.* 2002). Severe losses of diversity along streams and their riparian zones, and the lack of ecological improvement after costly restoration programmes (Verdonschot & Nijboer 2002; Jähnig *et al.* 2010; Brederveld *et al.* 2011) call for detailed understanding of the regulation of species distributions and biodiversity in relation to the dynamic interactions of water flow, erosion and sedimentation, seasonality, and flood/dry cycles. Mechanistic understanding of the roles of the first stages of vegetation establishment across natural gradients of riparian conditions will be a major contribution to our knowledge of these threatened habitats, which can be applied in restoration projects. Fundamentally, it will help build a more complete general framework considering the mechanisms that drive plant distributions and biodiversity across environmental gradients.

The objective of our study was to evaluate and compare the contributions of the three main stages in plant recruitment (following seed arrival), i.e. germination, seedling survival, and seedling growth, to the development of vegetation patterns and plant diversity in stream riparian zones. Specifically, we evaluated how germination, seedling survival, and seedling growth are likely to affect interspecific differences in distributions of plant species across the riparian environmental gradient, and how this may influence vegetation patterns. To this end, we carried out a series of field experiments in which we distributed seeds and seedlings of a wide range of riparian plant species across the full riparian environmental gradient. These field experiments were conducted along lowland streams with a restored hydromorphology, enabling a direct coupling of results to measures of rehabilitation success in previously degraded streams and riparian zones.

MATERIALS AND METHODS

We quantified germination, seedling survival and seedling growth of 17 native riparian plant species common to north-west Europe (Table 3.1) by introducing their seeds and seedlings across hydrological gradients in the riparian zones of three restored lowland streams (Fig. 3.1) in The Netherlands.

Study system

Riparian zones form the interface between aquatic and terrestrial environments, and comprise the area between the low and (extremely) high water marks (Naiman & Décamps 1997). They are characterized by strong environmental gradients, natural flooding disturbances, and a high connectivity, with consequently a high biodiversity

(Gregory *et al.* 1991; Naiman & Décamps 1997; Ward 1998). Lowland streams are widely distributed globally, but generally restricted to areas <200 m above sea level (Meybeck *et al.* 2001). In comparison with mountain streams, lowland streams generally occur in gently sloping valleys (0–5‰ slope). Being fed mainly by rainwater, lowland streams show a smoothed relation between precipitation patterns and discharge, with low flow velocities (0.05–0.6 m s⁻¹) (Verdonschot & Nijboer 2002).

In the Netherlands, lowland streams occur in the Pleistocene areas in the central, eastern, and southern parts of the country (De Vries 1976). These areas have a surface layer of Aeolian sand deposits and are located directly upstream of a large river delta (the Rhine–Meuse delta), running towards the North Sea. Over the past century, increasing population densities, and strong incentives for the regulation of water tables and stream hydrology have resulted in the channelization of almost all streams in the area. In recent years, recognition of the strongly diminished water retention, as well as high riparian biodiversity losses, have stimulated measures aimed at preserving and restoring the natural hydrology and morphology of the streams and their riparian zones, with variable success (Verdonschot & Nijboer 2002; Jähnig *et al.* 2010; Brederveld *et al.* 2011).

We selected three lowland streams in the Netherlands—the Hagmolenbeek (HM; 52°13'0.33" N, 6°43'16.88" E), Hooge Raam (HR; 51°42'57.65" N, 5°42'9.25" E) and Kleine Aa (KA; 51°35'39.92" N, 5°16'38.71" E). All had been subject to restoration measures along 0.8–2-km stretches of stream between 2009 and 2011. Restoration involved raising the stream bed, narrowing the channel, and excavating the gradually sloping riparian zones down to bare sand. A meandering watercourse was recreated in two of the streams (HM and KA, Fig. 3.1). All vegetation was still in a very early successional stage during the experiments, which took place 1–2 years after the restoration activities. More details on the research locations are available in Appendix A3.1.



Figure 3.1. Newly-developing riparian vegetation along a restored section of a Dutch lowland stream, the Kleine Aa, Boxtel, the Netherlands.

Field experimental set-up

Three replicate transects were laid out at each stream, perpendicular to the stream channel. Each transect consisted of one in-stream plot and four plots with increasing elevation along the riparian gradient (Fig. 3.2), with subsequent distances of ~ 0.5, 1.0, 3.0, and 5.0 m between plots 1–5 (low to high elevation). To avoid interference with the experiments, all plots were cleared of any (still very sparse) pre-existing vegetation. Two separate experiments were carried out in each plot—a seed germination experiment and a seedling survival/growth experiment (Fig. 3.2). Replicate transects were 25–50 m apart from each other, which was the maximum possible in the area available for research. A wide range of typical riparian plant species that are common to north-west European lowland stream valleys was selected for the experiments, representing plant species from across the entire riparian gradient (Table 3.1). Their Ellenberg F-values, used here as a quantitative approximation of the ecological optima for adult plants, range from 4 to 10, indicating optima at relatively dry conditions (F-value 4, indicating conditions ‘between dry and moist’), moist conditions (F-values 5–7), wet conditions (F-values 8–9), or in shallow water (F-value 10) (Ellenberg 1988;

modified for Britain by Hill *et al.* 1999). With two or three species for each Ellenberg F-value from 4 to 10, we aimed to include a balanced representation of riparian plant species with differing moisture preferences.

Table 3.1. Overview of species selected for the experiments, with seed sources, plant growth form, Ellenberg F-values (see 'Field experimental set-up'), total germination, seedling survival, and dry weight per planted seedling after 3 months, measured in the field experiments. Seed suppliers were (B) Biodivers, Oudewater, (C) Cruydhoeck, Nijeberkoop, (M) Medigran, Hoorn, all in the Netherlands, or (J) Jelitto, Schwarmstedt, Germany. Nomenclature and growth form according to van der Meijden (2005), with (Ch) chamaephyte, (Hc) hemicryptophyte, (He) helophyte, and (Th) therophyte. All species are perennial, except the annual *Geranium pusillum*.

Species	Supplier	Growth form	Ellenberg F-value	Germination tot (%)	Survival tot (%)	Dryweight tot (g)
<i>Ranunculus lingua</i>	B	He	10	29	66	0.06
<i>Berula erecta</i>	B	He	10	24	39	0.02
<i>Glyceria maxima</i>	J	He	10	14	67	0.04
<i>Myosotis scorpioides</i>	M	Hc/He	9	24	76	0.17
<i>Ranunculus flammula</i>	J	Hc/He	9	20	67	0.07
<i>Lycopus europaeus</i>	C	Hc/He	8	12	52	0.04
<i>Phalaris arundinacea</i>	C	Hc/He	8	11	86	0.13
<i>Lotus pedunculatus</i>	C	Hc/He	8	26	68	0.41
<i>Succisa pratensis</i>	C	Hc	7	12	66	0.05
<i>Ranunculus repens</i>	C	Ch/Hc/He	7	06	69	0.12
<i>Festuca pratensis</i>	M	Hc	6	13	79	0.10
<i>Anthoxanthum odoratum</i>	C	Hc	6	24	71	0.17
<i>Alopecurus pratensis</i>	C	Hc	5	15	83	0.08
<i>Trifolium repens</i>	C	Hc	5	17	52	0.31
<i>Rumex acetosa</i>	C	Hc	5	23	65	0.09
<i>Tragopogon pratensis</i> ssp. pr.	C	Hc	4	16	54	0.04
<i>Geranium pusillum</i>	C	Th	4	11	14	0.01

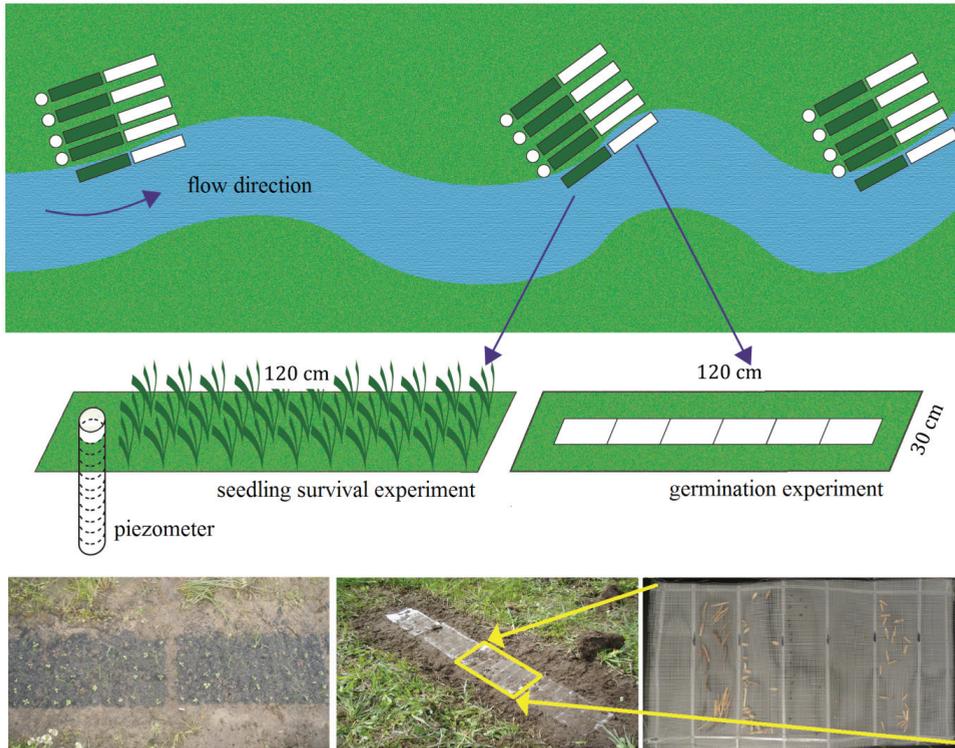


Figure 3.2. Overview of the experimental set-up in the field. Three replicate transects were laid out per stream, each transect consisting of one in-stream plot and four plots at increasing elevations along the riparian gradient. At each plot, two experiments were performed—a germination experiment, with introduced seeds in mesh bags; and a seedling survival and growth experiment with introduced seedlings. Piezometers were installed to register phreatic water levels at each plot.

Germination experiment

For the germination experiment, two sets of 20 seeds per species were placed on the sediment of each of the plots. To keep the seeds in the plots, they were enclosed in polyester mesh bags (mesh size 680 μm , thread diameter 150 μm , with parallel compartments of 8 \times 4 cm keeping seeds of single species together; Fig. 3.2), which were pinned to the soil. The first set was collected after 2 months in the field and taken to the laboratory to score germination. The second set was collected 1 month later to evaluate the effect of minor environmental fluctuations over time. All seeds were purchased from commercial suppliers of wild plant seeds (Table 3.1). Seeds of these companies are commonly used in re-introduction projects and are typically either collected from natural wild populations or are still very closely connected to wild populations by minimising the amount of produced generations (mostly only one

generation). All seeds were chilled at 4°C in the dark for at least 1 month before use. The experiments ran from May to August in 2012 (and for nine species at HM and HR in 2011).

A greenhouse experiment was performed to compare the germination of seeds enclosed in mesh bags with a control group (20 seeds per species, three replicates per group). This was done under 'field capacity' (the amount of water left in the sediment when excess water has been drained) and 'waterlogged' conditions (water-saturated sediments), representing two realistic field moisture conditions. Results showed that, in contrast to a study with slightly different mesh bags (Sarneel & Soons 2012), enclosing seeds in mesh bags lowered germination proportions for all species on average (\pm SD) from 0.50 (\pm 0.23) to 0.30 (\pm 0.22) under field capacity, and from 0.56 (\pm 0.28) to 0.41 (\pm 0.19) under waterlogged conditions. Crucially, the effect of mesh bags was similar between moisture treatments. A generalized mixed effects model with binomial error structure (glmmPQL, *Mass* package; Venables & Ripley 2002) and species as a random factor (intercepts) showed significant effects of moisture treatment ($t = 3.350$, $p = 0.001$) and mesh bag usage ($t = 5.858$, $p < 0.001$), but no significant interaction ($t = -1.127$, $p = 0.261$). Therefore, we assume that mesh bags reduced total germination proportions in the field experiments, but did not influence patterns in germination.

Seedling survival and growth experiment

To assess the contributions of the processes of seed germination, seedling survival and growth, we used plants at the seedling stage that had been grown from seeds of the same origin as those in the germination experiment. Ten seedlings per species were transplanted to each plot in the field from seedling trays (plastic trays of 50 × 28 × 3 cm composed of 3 × 3 × 3-cm cups, with water- and root-permeable bottoms) in which they had germinated in a plastic greenhouse (conditions similar to outside without precipitation). To minimize disturbance of roots, 3–4-week-old seedlings were transplanted together with some substrate (a 1:1 mixture of sand and potting soil) into every plot. Seedlings were arranged in a rectangle of 120 × 20 cm (Fig. 3.2) within the plot, with 3.5 cm distance between individual seedlings. Seedlings were randomly distributed to minimize possible effects of within-plot differences in soil conditions. Seedling survival was scored after 2 weeks and 1, 2, and 3 months. Living shoots were harvested after 3 months to measure biomass (above-ground weight after drying at 70°C for 48 h). The seedlings were in the field from June to August 2012. For *Geranium pusillum*, *Glyceria maxima*, and *Ranunculus flammula*, the seedling survival experiment could not be carried out at HM due to the limited availability of seedlings at the time.

Abiotic environmental conditions

To quantify the hydrological conditions along the riparian zones studied, water tables and surface water levels were continuously monitored using barometrically-compensated pressure transducers (Schlumberger Water Services, Delft, the Netherlands; Keller Meettechniek B.V., Reeuwijk, the Netherlands) in 1–2 m deep piezometers (Fig. 3.2) and water level gauges. Soil volumetric water content (0–10 cm depth) was measured at upper (non-saturated) plots of transects with 10-HS soil moisture probes (Decagon Devices Inc., Whitman County, WA, USA). All measurements were performed on an hourly basis, with average values during the experimental periods used for further analyses. Organic matter content, particle size distribution and nutrient availability (extractable N and P) were measured on three combined soil cores (4 cm diameter, 10 cm depth) per plot before starting the experiments. Methodological details are given in Appendix A3.2.

Data analysis

The responses of plant species (germination percentage, survival percentage, and biomass) to water level and other abiotic variables across the gradient showed strong non-linear patterns. Because non-linear patterns are not supported in regular generalized linear (mixed) models, smoothing functions on predictor variables (splines) are widely used as an extension of such models (see Zuur *et al.* 2009 for more details). We used P-splines (Marx & Eilers 1998), because of their flexibility in choice of reference curve (constant, straight line, or parabola) as explained in more detail in Appendix A3.3. Specifically, we used Bayesian P-splines (Lang & Brezger 2004), because they better acknowledge the uncertainty in smoothing parameters than marginal maximum likelihood (MML) used in most other approaches. For fitting Bayesian P-splines in generalized linear mixed models (GLMM) we used the R package INLA (Rue *et al.* 2014).

To analyse the numbers of individuals that germinated and survived in relation to water level and other abiotic variables, we used GLMMs with a logistic link and a beta-binomial error distribution. We used the beta-binomial (instead of the binomial) error distribution to account for over-dispersion in the data. To analyse biomass, we log-transformed the data to improve normality, and modelled the data with GLMMs using the identity link and a normal error distribution. Transects were included as random effects (intercepts) in all models. Although transects were nested within streams in our experimental design, streams were not included as an additional random effect. Exploratory analyses confirmed that, with transects being a finer grouping level in our experimental design than streams, we captured the largest part of variability imposed by the multilevel design. We compared the performance of GLMMs with different abiotic variables included by using the INLA estimate of the

deviance information criterion DIC, which is the Bayesian counterpart of Akaike's information criterion AIC (Spiegelhalter *et al.* 2002), and combines data fit and model complexity in a single measure. Lower DIC values indicate more parsimonious models. A rule of thumb for using DIC in model selection is that 'a difference of more than 10 rules out the model with the higher DIC while with a difference of less than 5 there is no clear winner' (Lesaffre & Lawson 2012).

As a final step, we applied a multivariate analysis to test whether the hydrological gradient affected the composition of the emerging and surviving seedling community. The effect of germination on the community composition was analysed using partial canonical correspondence analysis as it showed a unimodal response. Effects of log-transformed seedling survival and growth were analysed using partial redundancy analysis, with transect partialled out in all analyses. Overall significance was tested with permutation tests (1999 permutations). Data of six plots were excluded from multivariate analyses on all three processes due to missing values, as well as two species (*Lotus pedunculatus* and *Trifolium repens*) for germination, and three species (*G. pusillum*, *G. maxima*, and *R. flammula*) for seedling survival and growth. Multivariate analyses were performed in Canoco 5.04 (ter Braak & Šmilauer 2012). All other analyses were performed in R 3.0.3 (R Core Team 2014), using ggplot2 for graphs (Wickham 2009).

RESULTS

General patterns in germination, seedling survival, and seedling growth

Almost all species showed clear patterns in germination, seedling survival, and seedling growth along the riparian gradient (Fig. 3.3), even though there were strong interspecific differences in overall (averaged) performance for the three recruitment stages (Table 3.1). Statistical models fitted to the data unequivocally demonstrate that all three recruitment processes were primarily affected by the hydrological conditions along the riparian gradient (measured as local water levels). For all species and recruitment processes, DIC values of the models improved by far the most when water level was added as an explanatory variable. When additional explanatory variables were added in a forward regression, model improvement was either absent or very small (Appendix A3.4).

For each species, germination showed a clear optimum at some point along the hydrological gradient, with more or less gradual declines towards the wet and dry ends. Almost all species showed relatively high seedling survival across a wide range of intermediate water levels, with a steep decline under flooded conditions, and a weaker decline at the drier end of the gradient. Seedling growth showed patterns with clear and relatively narrow optima, or an exponential decline from dry to flooded

conditions (Fig. 3.3 and Appendix A3.5).

While the water level along the riparian gradient was the factor that explained most of the variance in the three recruitment processes, organic matter content, N availability or P availability explained additional variances in a forward regression (delta DIC below -5) for either one or two species per recruitment process (Appendix A3.4). The general effect on recruitment of these species was that higher values of these additional variables slightly stimulated recruitment processes. Under very high N availabilities (above 7.5 and 2.7 mg kg⁻¹ dry soil, respectively), however, seedling survival and growth were again reduced (data not shown).

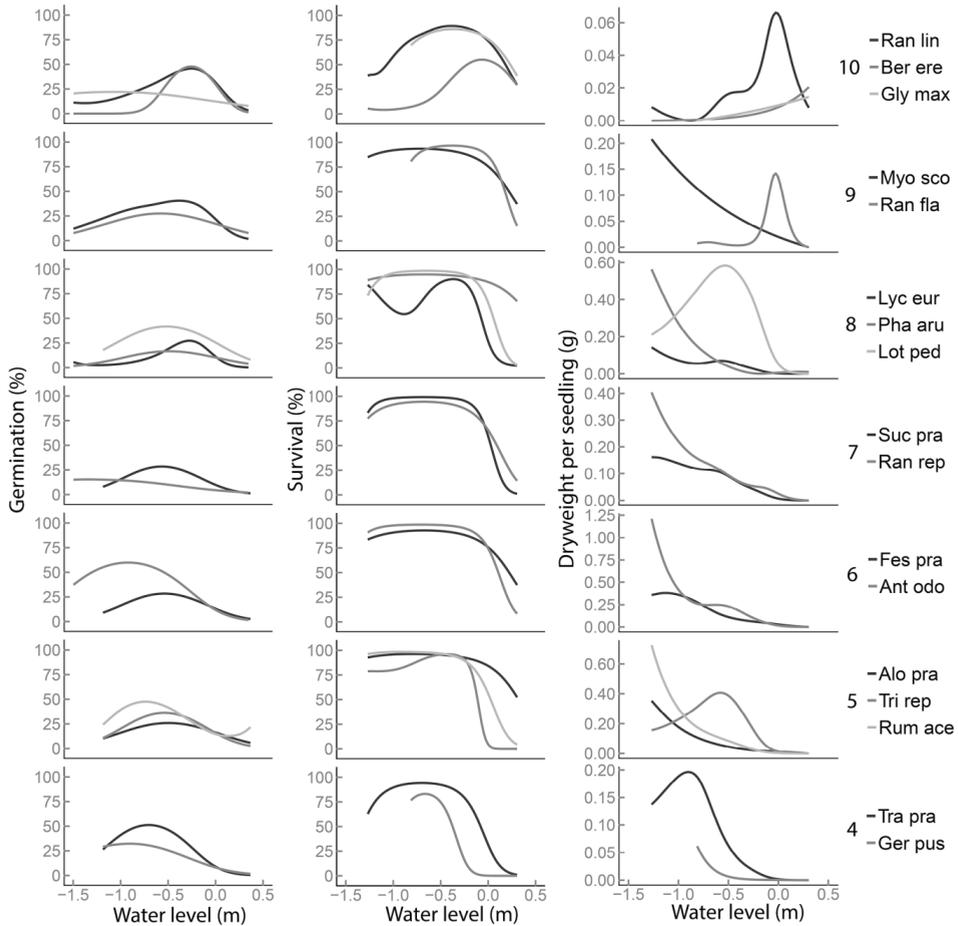


Figure 3.3. Species-specific patterns in germination (left), seedling survival (centre), and seedling growth (right) along the riparian gradient, as projected by the statistical models fitted to the field data (see 'Data analysis'). Negative water level values indicate that the water table lies below the soil surface; positive values indicate it is above the soil surface (flooding). Plant species are indicated by different line shades as explained by species name abbreviations on the right and are grouped by Ellenberg F-values, sorted from 10 (very wet; top) to 4 (relatively dry; bottom), also indicated on the right.

Differences between species

As detailed above, almost all species showed clear optima for germination and seedling growth along the riparian gradient and a wider range of optimal conditions for seedling survival. The optima of these curves (medians of the water level ranges in which predictions exceeded 75% of the maximum) along the hydrological gradient varied strongly between species (Fig. 3.3), in accordance with species' Ellenberg F-values, which indicate the species' optima as adult plants. Notably, the species-specific optima for germination showed a clear positive linear relation with the species' Ellenberg F-values (Fig. 3.4). For seedling survival and growth this relationship was different, showing almost no relationship between recruitment optima and adult optima across a wide range of lower Ellenberg F-values, but interestingly, a strong exponential increase tightly linking the two optima for species with higher Ellenberg F-values (Fig. 3.4).

Effects on species composition

The species-specific variation in the response curves clearly affected the composition of the emerging and surviving seedling community along the hydrological gradient. Canonical correspondence analysis on germination, and redundancy analysis on seedling survival and growth, showed significant changes in community composition with water level as the strongest predictor (total adjusted explained variation 28.4, 36, and 50% for germination, seedling survival, and seedling growth, respectively, and $p = 0.002$ in all three analyses), as shown in Appendix A3.6.

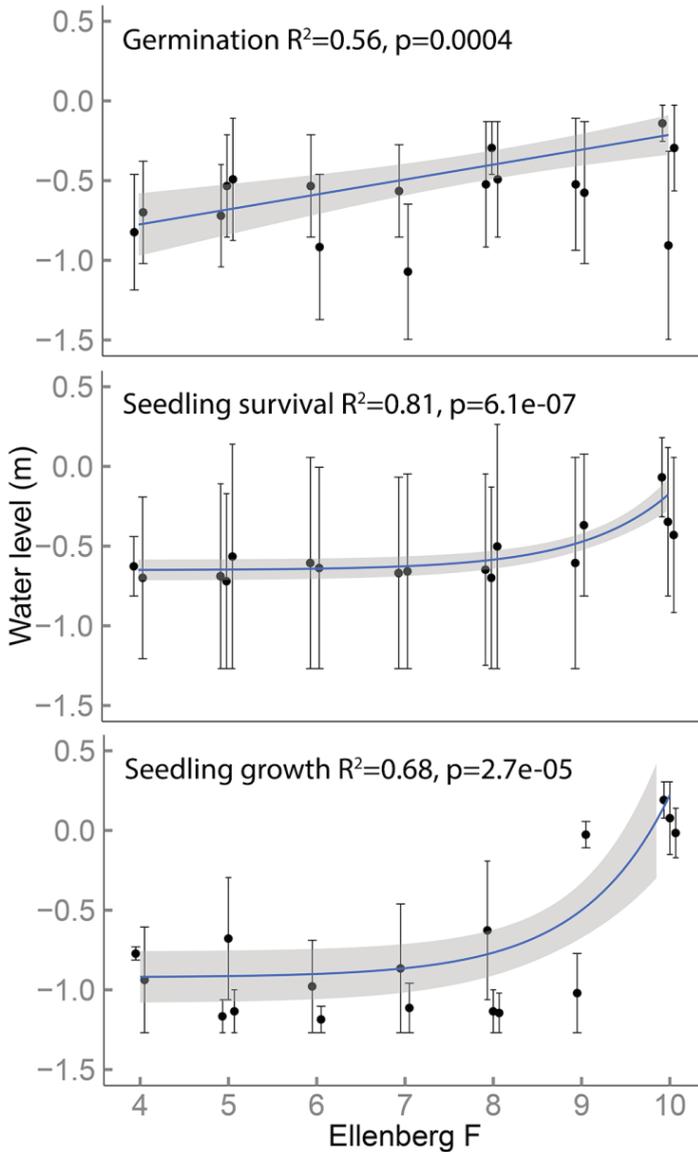


Figure 3.4. Species-specific environmental optima with respect to water level along the riparian gradient for germination (top), seedling survival (centre), and seedling growth (bottom). Negative water level values indicate that the water table lies below the soil surface; positive values indicate it is above the soil surface (flooding). The error bar indicates the range in which species response values are above 75% of the maximal predicted values and the filled circle is the middle of this range. Plant species are sorted by their Ellenberg F-values, from 4 (relatively dry) to 10 (very wet) with dodged positions along the x-axis. Blue lines indicate the expected values of inverse variance-weighted regressions (best fit between a linear or exponential function) on the medians, with shaded confidence intervals (95% CI) and regression statistics in the top left corner.

DISCUSSION

Environmental filtering effects on germination, seedling survival, and seedling growth

The three consecutive recruitment stages following seed arrival (i.e. seed germination, seedling survival and seedling growth) all responded very strongly to local hydrological conditions along the riparian gradient of the restored lowland streams. All three recruitment stages showed strong abiotic limitations at the wetter end of the gradient. At the dry end of the gradient, low water availability corresponded to limited germination and, for some species, survival and growth. Likely mechanisms underlying these patterns are that flooding induces anoxic conditions, reduces light and carbon dioxide, and may bury seeds, which may hamper germination and limit plant growth (Colmer & Voeselek 2009; Burmeier *et al.* 2010; Fraser *et al.* 2014). Waterlogging may additionally inhibit recruitment by increasing fungal mortality of seeds (Schafer & Kotanen 2003) and inducing plant toxicities (e.g. by reduced soil components accumulating to toxic levels in root tissues, or by acid loads injuring root cells; Colmer & Voeselek 2009). Under dry conditions, low water availability has been shown to hamper seed imbibition (Evans & Etherington 1990), induce seedling mortality (Grime & Curtis 1976), and suppress growth (Haugland & Froud-Williams 1999), thereby reducing recruitment.

Other environmental factors appeared to play virtually no role. In a few cases, higher organic matter contents correlated positively with germination and survival, probably by stimulating soil water-holding capacity (Haugland & Froud-Williams 1999), which may benefit species with higher moisture requirements (Evans & Etherington 1991). And for a few species, higher N and P availability correlated positively with recruitment, as has been previously reported for germination (Peterson & Bazzaz 1978) and growth (Güsewell 2004), although very high concentrations may inhibit recruitment through increased competition for light (Güsewell *et al.* 2003) or ammonium sensitivity (Dorland *et al.* 2003). All combined, our results demonstrate that water level is the main determinant of recruitment success across riparian gradients of lowland sandy streams, affecting all three consecutive recruitment processes following seed arrival. As such, water level acts as a strong environmental filter limiting species distributions along the riparian gradient.

While environmental filtering on germination and seedling growth was strong over the entire hydrological gradient, seedling survival was only clearly affected by flooding. Seedling survival therefore appeared to be of less importance in contributing to future vegetation patterns along the hydrological gradient than germination and seedling growth. This was surprising, as seedling survival has been assumed to be strongly affected by environmental conditions (Grubb 1977; Grime 2001), including

flooding (van Eck *et al.* 2004; Garssen *et al.* 2015) and drought (Garssen *et al.* 2014) in riparian zones. Perhaps, earlier studies focused particularly on the flooded part of the riparian zone, where seedling survival was strongly inhibited also in our experiments. High survival rates at the drier end may have been facilitated by the absence of extreme droughts during our experiments. Soil moisture contents reached 30% in the driest plots (and down to 20% on the driest days), but did not reach the critical 15% which has been shown to reduce growth for grassland species (Haugland & Froud-Williams 1999). Thus, drought stress at the upper end of lowland stream riparian zones in an Atlantic climate, such as in north-west Europe, may not be a limiting factor for the survival of many riparian species.

Contribution of recruitment processes to plant species distributions, vegetation development, and biodiversity

Multivariate analyses confirmed that environmental filtering was species-specific, resulting in changes in species composition of the emerging and growing plant communities along the hydrological gradient. These results unequivocally demonstrate that environmental filtering already initiates niche segregation during the three early recruitment stages, and not only operates during the adult stage of the plants' life cycle, e.g. through competitive interactions (Wedin & Tilman 1993). Such effects have hardly been reported yet for recruitment processes in a field setting (we are only aware of Lenssen *et al.* 1999, who investigated different functional groups). Most importantly, our results demonstrate that all further steps in vegetation development do not operate on a neutral combination of plant species, but on a pre-defined template, set by the early recruitment processes germination, seedling survival and growth.

Strikingly, analyses on species-specific recruitment patterns along the hydrological gradient revealed strong positive relationships between species recruitment optima and their Ellenberg F-values, which indicate the optimal moisture status of adult individuals in fully developed vegetation (Ellenberg 1988; modified for Britain by Hill *et al.* 1999). For species with higher Ellenberg F-values (indicating adult optima at wetter conditions), recruitment optima for germination, seedling survival and growth were clearly located at the wetter end of the riparian gradient, while germination of species with lower Ellenberg F-values (indicating adult optima at drier conditions) was optimal at the drier end of the gradient. Although Ellenberg indicator values are approximations on an ordinal scale, rather than measured optima on a linear scale, the Ellenberg F-values we used are based on independent, intensive field surveys (Hill *et al.* 2000). It is remarkable that they relate so clearly to the performance during early recruitment stages in a plant's life cycle. These results suggest that at least some riparian plant species may have evolutionary adaptations that promote recruitment under favourable hydrological conditions for adult growth and reproduction. Selective

recruitment along hydrological gradients corresponding to adult distribution patterns have been previously reported in greenhouse studies (Keddy & Ellis 1985; Evans & Etherington 1990, 1991) and along stagnant water systems (Sarneel *et al.* 2014b), supporting a wider applicability of these relations across hydrological gradients.

The exponential instead of linear relationships between recruitment optima and Ellenberg F-values for seedling survival and growth can be explained by the relatively mild drought conditions (see above), which only inhibited species with high Ellenberg F-values. This, in combination with relatively wide tolerance ranges of *P. arundinacea* and *M. scorpioides* (Weeda *et al.* 1988, 1994), may also explain the surprisingly high seedling growth at dry conditions for *M. scorpioides*, *L. europaeus*, and *P. arundinacea* (Ellenberg F 8–9).

In the analyses above, it has been our particular aim to elucidate the separate contributions of the three individual recruitment stages to the formation of plant species distributions, vegetation patterns, and biodiversity. Any multiplicative effects across early life-history stages (e.g. adaptations that promote germination of specific genotypes under certain conditions, which may also promote survival and growth of these genotypes under the same conditions) were excluded by using different individuals for our experiments on germination and seedling survival. If such multiplicative effects would strengthen each other, our results would even underestimate the combined importance of the early recruitment processes investigated for later vegetation patterns. Such analyses may be the next step in assessing the role of early recruitment stages.

Implications

The results of our experiments demonstrate that following a disturbance, early recruitment stages—and especially seed germination and seedling growth—already initiate niche segregation and the development of vegetation patterns along the riparian hydrological gradient. From a theoretical perspective, this supports (and quantifies) the importance of ‘regeneration niches’ in determining the extent to which adult plants can realize potential niche occupation (Grubb 1977). Moreover, the results indicate that early recruitment processes may contribute significantly to the hydrological niches that form the basis for species coexistence along hydrological gradients (Silvertown *et al.* 1999). From an applied perspective, these results suggest that wider and more gradual (i.e. more natural) riparian zones can accommodate more species-specific recruitment requirements. Conserving or restoring this natural riparian habitat heterogeneity is therefore likely to promote species coexistence and biodiversity. Flooding, and associated successional setbacks, may further stimulate species coexistence (Pollock *et al.* 1998; Shea *et al.* 2004), and distribute seeds from local populations (Nilsson *et al.* 2010), important prerequisites to achieving diverse

vegetation patterns when riparian habitats are restored (Verhoeven *et al.* 2008; Brederveld *et al.* 2011).

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DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.mv13v>.

Appendix A3.1. Research locations, additional information

The field experiments were performed at three lowland streams in the Netherlands (Fig. A3.1.1). All streams had been subject to restoration measures along 0.8–2-km stretches of the stream. Restoration activities at the Hagmolenbeek (HM) were completed in June 2010, at the Hooge Raam (HR) in July 2009 (only the channel) and April 2011 (the riparian zone), and at the Kleine Aa (KA) in July 2011. Transversal profiles after restoration differed between the streams, with channel widths/depths of 2.0/0.3, 7.0/0.2, and 7.0/0.8 m, and riparian zones widths of 25, 15, and 10 m for HM, HR, and KA, respectively. Hydrological conditions varied accordingly, with average hourly discharges of 0.12, 0.15, and 0.85 m³ s⁻¹, peak discharges of 1.03, 1.64, and 7.2 m³ s⁻¹, and overbank flows amounting to 109, 59, and 139 days, all for the year 2012, except discharge values at KA (March 2013–December 2013). At HM only, the riparian zone was sown with a seed mixture of *Lolium perenne*, *Trifolium repens*, and *Phleum pratense* subsp. *pratense* (van der Meijden 2005), to reduce possible erosion after restoration.



Figure A3.1.1. Pictures of the three research locations, showing the excavated riparian zones shortly after the restoration measures.

The experiments were performed shortly after the streams and riparian zones had been excavated to bare sand. Therefore, at the start of our experimental introductions, naturally-developing vegetation cover was still very low at HR and KA. At HM a more developed (yet still relatively sparse) vegetation occurred due to the above-mentioned sowing. To avoid interference with our experiments, all pre-existing vegetation was removed from all plots. Soil data were collected from all plots to analyse the differences in pretreatment conditions, as described in the Methods section.

Appendix A3.2. Soil analyses

Organic matter content was determined by loss on ignition of dry soil samples at 550°C for 2.5 h. The remaining mineral soil fraction (approximately 5 g) was treated with 0.1 M HCl for 24 h to remove carbonates, neutralized with demineralized water, and wet-sieved in particle size classes: <20, 20–53, 53–100, 100–160, 160–200, 200–250, 250–500, >500 µm. A weighted average particle diameter was calculated from these categories (with 20 and 500 µm for the <20 and >500 µm size classes) as in Youker & McGuinness (1957). Extractable phosphate was determined by extracting P with 0.5 M NaHCO₃ at pH of 8.5 (Olsen *et al.* 1954), followed by a colorimetric measurement using molybdate-ascorbic acid (Murphy & Riley 1962). Extractable ammonium and nitrate were determined with 0.4 M KCl extraction (Houba *et al.* 1995), followed by a colorimetric measurement on a continuous flow analyser (Skalar SA-40).

Appendix A3.3. Statistical methods

The responses of plant species (germination percentage, survival percentage, and biomass) to water level and other abiotic variables across the gradient showed strong non-linear patterns. Because non-linear patterns are not supported in regular generalized linear (mixed) models, smoothing functions on predictor variables (splines) are widely used as an extension of such models (see Zuur *et al.* 2009, for more details). We used P-splines (Marx & Eilers 1998) because of their flexibility in choice of reference curve (constant, straight line, or parabola). The most commonly used approach models a spline as deviation from a straight line. However, ecological niche theory suggests that responses can be unimodal along environmental gradients, so that a natural reference model is the Gaussian response curve (Jongman *et al.* 1995), which is a parabola on the link scale of a generalized linear (mixed) model. Specifically, we used Bayesian P-splines (Lang & Brezger 2004), because they better acknowledge the uncertainty in smoothing parameters than marginal maximum likelihood (MML) used in most other approaches. For fitting Bayesian P-splines in generalized linear mixed models (GLMM) we used integrated nested Laplace approximation (Rue *et al.* 2009), as implemented in the INLA R package (Rue *et al.* 2014) and a dedicated R-function. All technical details on this method are described below under 'Bayesian P-splines using INLA'.

To analyse the number of individuals that germinated and survived in relation to water level and other abiotic variables, we used GLMMs with a logistic link, and a beta-binomial error distribution. We used the beta-binomial instead of the binomial error distribution to account for over-dispersion in the data (or to allow for pairwise correlation (r , $0 < r < 1$) between the germination and survival of individual seeds in the same plot). The beta-binomial occasionally led to numerical problems in cases with many observations close to 0 or to the binomial total (10 for survival), in which case we set the distribution to binomial (see Appendix A3.4). To analyse biomass, we log-transformed the data to improve normality, and modelled the data with GLMMs using the identity link and a normal error distribution. Transects were included as random effects (intercepts) in all models to allow for overall differences between transects or to allow for correlation among samples from the same transect. Although transects were nested within streams in our experimental design, streams were not included as an additional random effect. Exploratory analyses confirmed that with transects being a finer grouping level in our experimental design than streams, we captured the largest part of variability imposed by the multilevel design, while obtaining more stable results.

More than a single abiotic variable can be added to the model to form a generalized additive model (Marx & Eilers 1998), and we did so to investigate the additional influence of these on the response. As the model is Bayesian and also

contains the random factor transect, the model could be called a Bayesian generalized additive mixed model (BGAMM). Comparison of models with a different number of abiotic variables was performed by using the INLA estimate of DIC, which is the Bayesian counterpart of AIC (Spiegelhalter *et al.* 2002), and combines data fit and model complexity in a single measure. Lower DIC values indicate more parsimonious models. A rule of thumb for using DIC in model selection is that ‘a difference of more than 10 rules out the model with the higher DIC while with a difference of less than 5 there is no clear winner’ (Lesaffre & Lawson 2012).

Bayesian P-splines using INLA

In brief, P-splines consist of a cubic B-spline basis of the abiotic (predictor) variable with a large number of knots (in our case 20) and a penalty matrix that determines the amount of deviation from a reference curve, e.g. a horizontal line (constant), a straight line or a parabola (Eilers & Marx 1996). We used P-splines within a generalized linear mixed model context (Marx & Eilers 1998; Jiang 2007), where the reference curve applies to the link scale. In our models, we used a parabolic reference curve for the number of individuals germinated and survived, with higher values of the penalty yielding predictions closer to the reference curve (bell-shaped Gaussian logistic curve; Jongman *et al.* 1995) and lower values of the penalty allowing asymmetric unimodal curves. For the logarithm of biomass, we used a straight line reference.

The reference curve is the result of the fact that the penalty is imposed on increments of the coefficients of a regression model with predictors formed by a B-spline basis of the abiotic variable. The order of the increments is equal to the order of the difference penalty. For example, if the first order increments (i.e. the differences) are all zero, the resulting curve is a horizontal line. P-splines based on mixed models often under-smooth, as mixed models often do for variance components (Jamil & Ter Braak 2012). In Bayesian P-splines, the amount of smoothing can be steered in an indirect way by the prior, for which we take the newly-developed penalized complexity (PC) prior (Martins *et al.* 2014). This translates to a type 2 Gumbel prior distribution for the penalty parameter (which is a precision or inverse variance) or, equivalently, an exponential prior distribution with rate λ for the standard deviation of the normal distribution of the B-splines coefficient increments. We assumed an a priori marginal standard deviation of the increments of 1 yielding $\lambda = 1.427$ (Martins *et al.* 2014). As transects are likely to differ, we did not use a PC prior for the variance of the transect-dependent intercepts, but instead used the usual inverse gamma (IG) prior, namely $IG(1, 0.01)$. For the beta-binomial distribution we used the default INLA prior (April 2014) for logit (r), which is a normal distribution with mean 0 and variance 2.5.

INLA implementation

The implementation of the Bayesian generalized additive mixed model in INLA utilizes the A-matrix approach (Martins *et al.* 2013), the essential idea of which is shown in Fig. A3.3.1. Fig. A3.3.1 hides all detail about priors, in order to obtain more readable code, uses the `bbase` function shown in Fig. A3.3.2 and does not use an explicit intercept. The file 'BayesianPsplines_1.0.tar.gz' (available online; Appendix S7 in Fraaije *et al.* 2015) is an R library and contains an example R script 'BayesPspline.r' in the demo folder. The user function `smooth_inla`, which does contain an explicit intercept, allows an additional random factor and additional abiotic variables. The library file contains a `readme.txt`, with additional explanation.

```

smooth_inla0 <- function(x,y, family, hyperB,
  xrange= c(0,1), diff.order = 2, ngrid = 100, nseg = 20, degree = 3 ){
# tutorial code showing how to fit a single spline
# Prepare basis and penalty matrix
  B = bbase(x, xrange[1], xrange[2], nseg, degree)
  D = diff(diag(ncol(B)), diff = diff.order)
  P = t(D) %*% D

# specify the linear combination for predictions on a grid
  x_grid = seq(xrange[1], xrange[2], length = ngrid)
  B_grid = bbase(x_grid, xrange[1], xrange[2], nseg, degree)

# In A-matrix approach, the output is c(eta*, eta), so shift B_grid...
  B_grid_plus =cBind(Matrix(0,nrow = nrow(B_grid), ncol =nrow(B)),B_grid)

# set up INLA call using the A-matrix approach
  mod.P = inla(
y ~ -1 + f(id.b, model="generic", Cmatrix = P, constr = F, hyper = hyperB),
data = list(y = y, id.b = 1:ncol(B)),
  control.predictor = list(A = B, compute = TRUE),
  lincomb = inla.make.lincombs(Predictor = B_grid_plus))
  Pred = mod.P$summary.lincomb.derived

  list(model_inla = mod.P, pred = Pred, x_grid = x_grid, B_grid=B_grid)
}

```

Figure A3.3.1. Skeleton of fitting a Bayes P-spline of predictor x to data y .

```

tpower <- function(x, t, p){
# Truncated p-th power function
(x - t) ^ p * (x > t)
}
bbase <- function(x, x1 = min(x), xr = max(x), nseg = 10, deg = 3){
# Construct B-spline basis

dx <- (xr - x1) / nseg
knots <- seq(x1 - deg * dx, xr + deg * dx, by = dx)
P <- outer(x, knots, tpower, deg)
n <- dim(P)[2]
D <- diff(diag(n), diff = deg + 1) / (gamma(deg + 1) * dx ^ deg)
B <- (-1) ^ (deg + 1) * P %*% t(D) B }

```

Figure A3.3.2. The function `bbase` for generating B-splines for a predictor x with range given by `xrange`.

Appendix A3.4. Relationships between recruitment processes and abiotic variables: model statistics and parameter selection

Table A3.4.1. DIC values for statistical models explaining germination, seedling survival, and seedling growth per plant species, with only transect (tr) as explanatory variable (random intercepts), and corresponding delta DIC values for the addition of either water level (wl), organic matter content (om), particle size (part), P availability (po4), or N availability (ntot) as fixed effect.

Germination

	tr	±wl	±om	±part	±po4	±ntot
Ran lin	459.2	-26.9	0.9	-0.4	2.2	-1.4
Ber ere	413.4	-45.1	1.8	-0.5	-1.5	-0.7
Gly max	357.3	-3.4	-1.2	-0.3	-2.3	1.1
Myo sco	431.5	-32.5	1.5	-0.6	1.0	2.4
Ran fla	375.0	-5.9	-0.4	-0.4	-0.9	-1.4
Lyc eur	291.5	-24.0	48.6	0.0	1.2	3.1
Pha aru	322.4	-16.1	1.3	-0.6	-4.3	3.6
Lot ped	364.4	-15.1	-1.8	-0.5	1.7	-0.1
Suc pra	321.9	-28.6	-3.6	-0.9	1.6	-1.7
Ran rep	240.5	-9.1	0.7	-0.4	-1.2	-2.4
Fes pra	356.4	-37.5	-12.5	-0.3	-0.3	-3.1
Ant odo	432.6	-74.2	2.9	-0.6	0.1	3.2
Alo pra	366.3	-27.2	-5.7	-0.5	1.3	2.8
Tri rep	281.3	-22.9	1.4	-0.6	1.9	0.2
Rum ace	422.9	-14.9	-1.9	0.2	1.9	-3.0
Tra pra	324.2	-54.1	0.2	2.9	0.8	0.1
Ger pus	300.6	-29.2	-1.6	-1.2	2.3	2.5
SUM	6061.4	-466.7	30.6	-4.7	5.5	5.2

Seedling survival

	tr	±wl	±om	±part	±po4	±ntot
Ran lin	184.1	-17.0	1.0	-0.5	0.8	-6.0
Ber ere	198.3	-17.0	-1.8	-0.5	-0.9	1.2
Gly max	123.7	-14.7	-3.5	-0.6	0.2	-1.8
Myo sco	179.3	-26.9	0.8	-1.7	1.4	0.7
Ran fla	117.4	-33.0	-0.5	-1.1	0.2	-4.3
Lyc eur	192.3	-48.9	-3.4	-0.4	-2.0	-5.4
Pha aru	140.3	-14.4	2.5	-0.5	-4.9	22.8
Lot ped	309.0	-215.3	-31.5	-0.1	-68.7	-55.4
Suc pra	329.5	-230.3	-63.1	0.0	-46.5	-49.0
Ran rep	179.8	-31.2	-6.5	-0.5	0.8	0.8
Fes pra	250.4	-162.4	-20.6	0.2	-36.5	-8.9
Ant odo	266.7	-169.1	-22.8	0.1	-43.8	-43.7
Alo pra	151.9	-25.1	3.2	-0.4	-0.8	-2.5
Tri rep	182.6	-84.7	-3.8	-0.4	-3.0	-0.4
Rum ace	323.4	-208.5	-44.4	0.0	-24.8	-53.5
Tra pra	175.1	-43.5	-2.2	-0.5	-2.8	-1.5
Ger pus	130.7	-84.8	-6.4	0.1	-1.0	Inf
SUM	3251.8	-1342.2	-199.1	-7.1	-229.6	-206.9

Seedling growth

	tr	±wl	±om	±part	±po4	±ntot
Ran lin	130.2	-3.0	-0.6	0.0	0.6	2.0
Ber ere	167.6	-16.9	-4.1	0.0	-0.5	3.1
Gly max	84.9	1.4	-4.4	0.0	1.6	3.3
Myo sco	127.9	-2.1	0.6	0.0	1.9	3.6
Ran fla	105.7	-21.3	-2.3	0.0	1.0	0.5
Lyc eur	178.3	-46.3	2.1	0.2	1.3	5.0
Pha aru	112.0	-23.7	1.2	0.0	2.8	2.3
Lot ped	189.9	-53.6	-6.4	0.3	5.4	-2.0
Suc pra	168.4	-87.9	-4.2	-0.1	1.3	-1.4
Ran rep	177.3	-27.7	-10.9	-0.1	1.6	1.0
Fes pra	144.8	-51.0	-1.2	0.0	2.3	2.3
Ant odo	189.8	-81.5	-3.1	0.0	1.2	-4.6
Alo pra	120.2	-29.0	1.5	0.0	2.3	3.8
Tri rep	175.4	-30.3	4.1	0.0	2.7	5.9
Rum ace	186.2	-84.4	-2.7	0.0	1.8	-0.3
Tra pra	139.8	-86.3	1.2	0.0	0.5	2.2
Ger pus	91.5	-40.1	1.1	0.0	2.6	3.3
SUM	2253.5	-592.5	-28.0	0.2	25.7	24.3

Species	Germination					Seedling survival					Seedling growth				
	tr±wl	±om	±part	±po4	±ntot	tr±wl	±om	±part	±po4	±ntot	tr±wl	±om	±part	±po4	±ntot
Ran lin	-26.9*	0.8	2.7	-1.6	-12.0*	-17.0*	-4.2	-4.7	-1.7	-12.3*	-3.0	2.2	0.0	2.3	2.7
Ber ere	-45.1*	2.4	0.3	0.4	1.5	-17.0*	-5.7*	4.9	0.1	-1.1	-16.9*	2.1	0.0	2.6	-4.6
Gly max	-3.4	-7.8*	-1.2	-1.6	5.1	-14.7*	4.0	0.0	1.7	7.7	1.4	-1.5	0.0	1.9	2.3
Myo sco	-32.5*	-0.9	-2.1	0.4	-2.5	-26.9*	-4.4	-0.3	-3.4	-2.6	-2.1	-2.0	0.0	2.7	1.7
Ran fla	-5.9*	2.4	0.8	-0.5	-0.9	-33.0*	4.7	1.1	2.4	1.1	-21.3*	2.5	0.2	4.4	2.3
Lyc eur	-24.0*	1.9	-1.2	4.0	0.5	-48.9*	-1.1	-1.8	-2.4	-0.9	-46.3*	-3.3	0.0	2.2	3.1
Pha aru	-16.1*	0.9	0.3	-2.6	2.6	-14.4*	-7.2*	-0.3	-3.0	-5.2*	-23.7*	2.3	0.0	0.2	2.5
Lot ped	-15.1*	-18.9*	-1.0	-0.8	0.4	(-215.3)	(-3.2)	(1.5)	(-1.4)	(-6.3)	-53.6*	-2.8	0.0	3.1	2.8
Suc pra	-28.6*	2.7	1.3	1.7	3.6	(-230.3)	(0.8)	(0.0)	(2.6)	(-5.4)	-87.9*	2.3	0.0	3.2	4.3
Ran rep	-9.1*	3.6	-0.2	2.1	3.2	-31.2*	2.1	-0.7	1.9	1.3	-27.7*	-1.1	0.0	1.2	3.5
Fes pra	-37.5*	1.5	0.5	-0.8	1.1	(-162.4)	(-17.0)	(-5.6)	(-3.5)	(2.3)	-51.0*	2.8	0.0	2.1	-0.7
Ant odo	-74.2*	3.4	1.5	3.0	1.4	(-169.1)	(-0.3)	(-1.2)	(3.9)	(-4.9)	-81.5*	-0.5	-0.2	-1.1	-10.1*
Alo pra	-27.2*	-1.8	-0.8	1.6	-0.8	-25.1*	0.6	-1.5	2.8	2.5	-29.0*	2.3	0.0	-0.5	3.9
Tri rep	-22.9*	2.0	0.2	0.6	0.2	-84.5*	3.7	-0.7	2.9	1.2	-30.3*	-1.5	0.0	-1.8	-22.7*
Rum ace	-14.9*	1.2	9.8	-6.8*	-21.7*	(-208.5)	(-5.4)	(-0.2)	(-0.2)	(3.4)	-84.4*	1.9	0.0	2.3	4.1
Tra pra	-54.1*	3.5	-0.3	1.1	-2.3	-43.5*	-1.1	-3.9	-6.4*	0.5	-86.3*	-2.2	0.0	1.1	2.0
Ger pus	-29.2*	3.1	0.1	3.8	-3.0	(-84.9)	(Inf)	(0.0)	(Inf)	(124.8)	-40.1*	3.6	0.0	0.5	-0.1
SUM	-466.7	0	10.7	4	-23.6	-356.2	-8.6	-7.9	-5.1	-7.8	-683.6	7.1	0.0	26.5	-3.3

Table A3.4.2. Delta DIC values for statistical models explaining germination, seedling survival and seedling growth per plant species, by the addition of water level to a model with transect (random intercepts) (tr±wl), and subsequent additions of either organic matter content (om), particle size (part), P availability (po4) or N availability (ntot) as fixed effects, to the model with transect and water level. Lower values indicate better predictive models, below -5.0 marked with an asterisk. For modelling seedling survival of 6 species, a binomial distribution was used, resulting in less reliable delta DIC values (indicated between brackets). These values were not marked with an asterisk and were excluded from the sum on the lowest row.

Appendix A3.5. Species-specific patterns in recruitment along the riparian gradient, with data and model fits shown per species

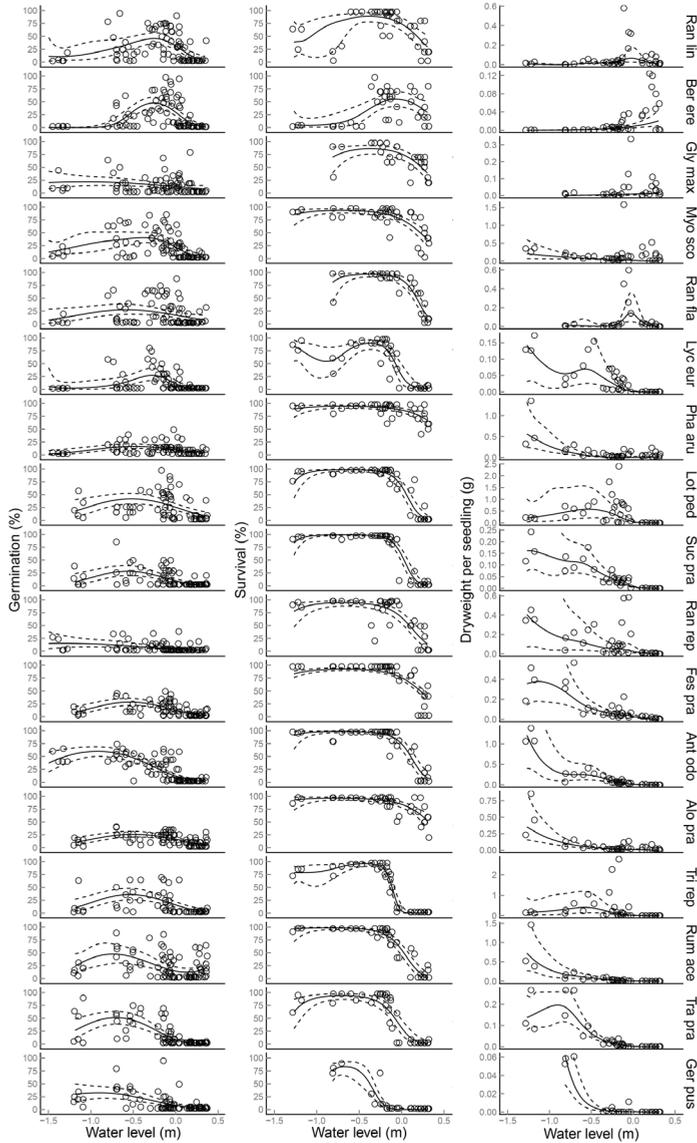


Figure A3.5.1. Species-specific patterns in germination (left), seedling survival (centre), and seedling growth (right) along the riparian gradient, with negative water level values indicating that the water table is below the soil surface and positive values indicating the water table is above the soil surface (flooding). Plant species are sorted by Ellenberg F-values, from 10 (very wet; top) to 4 (relatively dry; bottom), with their species names indicated on the right. Continuous lines represent best model fits to the field data (open circles), dotted lines represent 90% credible intervals of the modelled relationships (in equivalence with two-sides tests at the 5% level; van der Voet *et al.* 2011), which become wider with increasing model uncertainty.

Appendix A3.6. Multivariate analysis

Multivariate analyses were performed to test if environmental filtering across the hydrological gradient affected the species composition of the emerging and surviving seedling community. All explanatory variables (water level, N availability, P availability, particle size, organic matter content) were included in these analyses, with transect partialled out. Partial canonical correspondence analysis on germination explained 28.4% of the total variance (adjusted explained variation; $p = 0.002$, 1999 permutations), and partial redundancy analysis on log-transformed seedling survival and growth explained 36 and 50% respectively ($p = 0.002$, 1999 permutations). This demonstrated significant differences in community composition among plots along the riparian gradient, with water level as the strongest predictor for all three recruitment processes (Tables A3.6.1, A3.6.2, A3.6.3). Additionally, soil particle size was significant for germination, and organic matter content and P availability for seedling survival, all explaining much less of the variance than water level. Changes in community composition were visualized using distance triplots (Fig. A3.6.1, A3.6.2, A3.6.3): the closer species are together the more likely they co-occur (i.e. share similar responses) in the community (Fig. A3.6.1) or the more species point in the same direction the more similar their distribution (Fig. A3.6.2, A3.6.3).

Partial CCA on germination

Table A3.6.1. Overview of conditional effects in a partial canonical correspondence analysis on germination.

Variable	Explains %	pseudo-F	P	P(adj)*
Water level	11.9	3.9	0.002	0.010
Particle size	6.7	2.3	0.010	0.025
N availability	4.3	1.5	0.100	0.167
Organic matter content	2.6	0.9	0.724	0.724
P availability	2.8	1.0	0.664	0.724

* False discovery rate

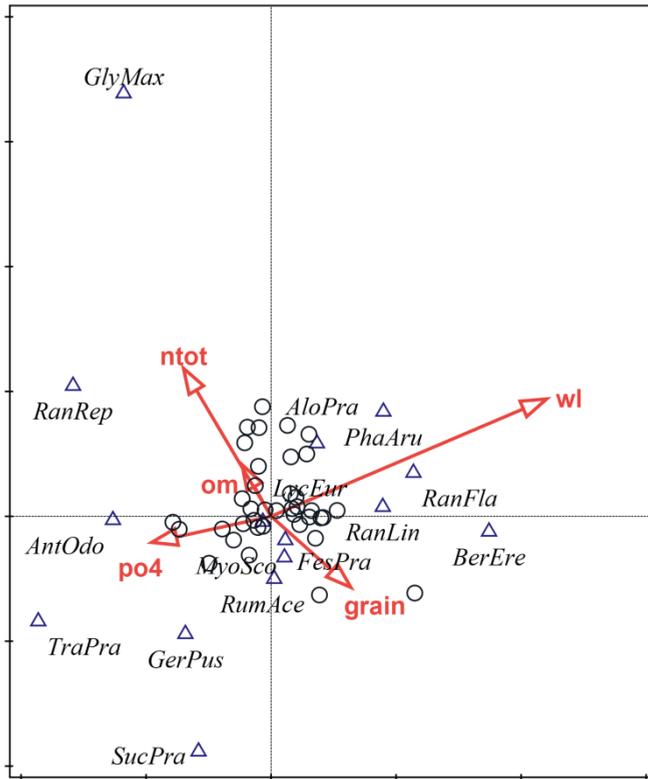


Figure A3.6.1. Distance triplot of the canonical correspondence analysis on germination, with respect to the environmental variables water level (wl), N availability (ntot), P availability (po4), particle size (grain), and organic matter content (om). Species scores are indicated with triangles and name abbreviation. Site scores are indicated with circles.

Partial RDA on seedling survival

Table A3.6.2. Overview of conditional effects in a partial redundancy analysis on log-transformed seedling survival.

Variable	Explains %	pseudo-F	P	P(adj)*
Water level	24.8	9.6	0.002	0.010
P availability	9.8	4.2	0.008	0.020
Organic matter content	9.3	4.4	0.018	0.030
Particle size	2.4	1.2	0.300	0.375
N availability	0.4	0.2	0.982	0.982

* False discovery rate

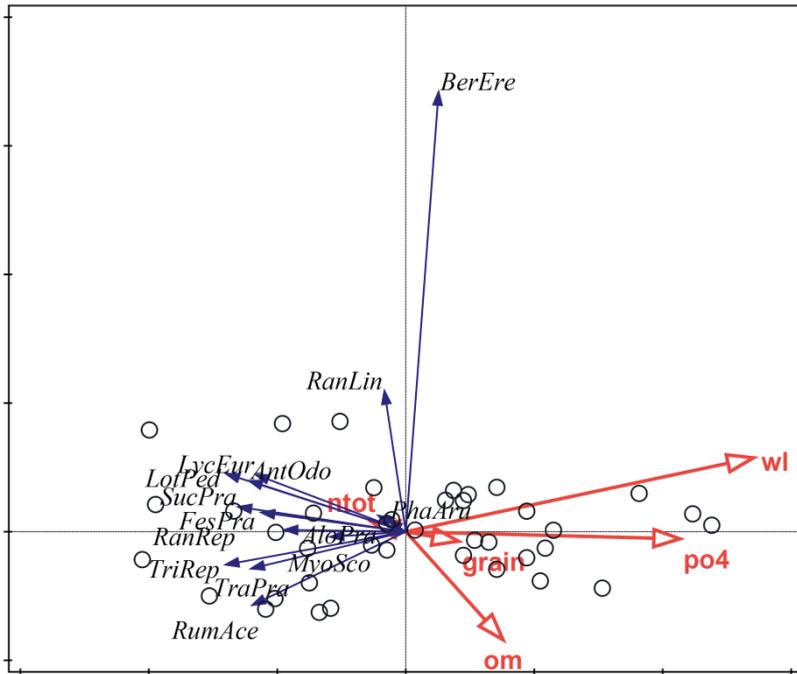


Figure A3.6.2. Distance triplot of the partial redundancy analysis on log-transformed seedling survival, with respect to the environmental variables water level (wl), N availability (ntot), P availability (po4), particle size (grain), and organic matter content (om). Species scores are indicated with arrows and name abbreviation. Site scores are indicated with circles.

Partial RDA on seedling growth

Table A3.6.3. Overview of conditional effects in a partial redundancy analysis on log-transformed seedling growth.

Variable	Explains %	pseudo-F	P	P(adj)*
Water level	41.5	19.8	0.002	0.01
P availability	7.0	3.7	0.114	0.1425
Organic matter content	5.2	2.9	0.064	0.10667
Particle size	4.7	2.8	0.04	0.1
N availability	0.3	0.2	0.968	0.968

* False discovery rate

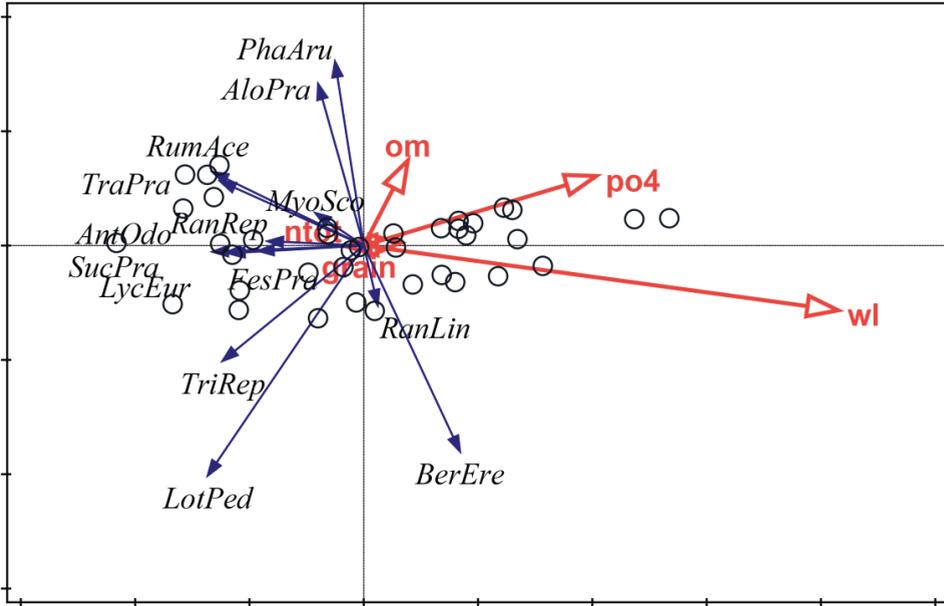


Figure A3.6.3. Distance triplot of the partial redundancy analysis on log-transformed seedling growth, with respect to the environmental variables water level (wl), N availability (ntot), P availability (po4), particle size (grain), and organic matter content (om). Species scores are indicated with arrows and name abbreviation. Site scores are indicated with circles.



Chapter 4

Dispersal *versus* environmental filtering in a dynamic system: drivers of vegetation patterns and diversity along stream riparian gradients

Rob G.A. Fraaije, Cajo J.F. ter Braak, Betty Verduyn, Jos T.A. Verhoeven and Merel B. Soons

ABSTRACT

Both environmental filtering and dispersal filtering are known to influence plant species distribution patterns and biodiversity. Particularly in dynamic habitats, however, it remains unclear whether environmental filtering (stimulated by stressful conditions) or dispersal filtering (during re-colonization events) dominates in community assembly, or how they interact. Such a fundamental understanding of community assembly is critical to the design of biodiversity conservation and restoration strategies.

Stream riparian zones are species-rich dynamic habitats. They are characterized by steep hydrological gradients likely to promote environmental filtering, and by spatiotemporal variation in the arrival of propagules likely to promote dispersal filtering. We quantified the contributions of both filters by monitoring natural seed arrival (dispersal filter) and experimentally assessing germination, seedling survival and growth of 17 riparian plant species (environmental filter) along riparian gradients of three lowland streams that were excavated to bare substrate for restoration. Subsequently, we related spatial patterns in each process to species distribution and diversity patterns after 1 and 2 years of succession.

Patterns in initial seed arrival were very clearly reflected in species distribution patterns in the developing vegetation and were more significant than environmental filtering. However, environmental filtering intensified towards the wet end of the riparian gradient, particularly through effects of flooding on survival and growth, which strongly affected community diversity and generated a gradient in the vegetation. Strikingly, patterns in seed arrival foreshadowed the gradient that developed in the vegetation; seeds of species with adult optima at wetter conditions dominated seed arrival at low elevations along the riparian gradient while seeds of species with drier optima arrived higher up. Despite previous assertions suggesting a dominance of environmental filtering, our results demonstrate that nonrandom dispersal may be an important driver of early successional riparian vegetation zonation and biodiversity patterns as well.

Synthesis: Our results demonstrate (and quantify) the strong roles of both environmental and dispersal filtering in determining plant community assemblies in early successional dynamic habitats. Furthermore, we demonstrate that dispersal filtering can already initiate vegetation gradients, a mechanism that may have been overlooked along many environmental gradients where interspecific interactions are (temporarily) reduced.

INTRODUCTION

Understanding the mechanisms that determine species distributions and biodiversity is a central goal in ecology. A major concept explaining species distributions is niche

differentiation by environmental filtering (Keddy 1992). According to this view, differences in species abilities to cope with abiotic constraints (Lenssen & de Kroon 2005) or compete for limiting resources (Tilman 1982) induce niche separation along environmental or temporal niche axes (Silvertown 2004). Dispersal filtering has also been raised as a major concept in explaining species distribution patterns, in which species distributions are explained by differences in arrival. According to this view, size of the local and regional species pools, chance colonization events and differences in species dispersal abilities are critical factors structuring plant communities (MacArthur & Wilson 1967; Zobel 1997; Hubbell 2001; Myers & Harms 2009).

Although there is general consensus that both concepts play a role in natural community assemblages (Gravel *et al.* 2006; Adler *et al.* 2007; Myers & Harms 2009; Götzenberger *et al.* 2012), the assessment of their relative importance across time, space, or ecosystem types remains challenging (Chase & Myers 2011; Shipley *et al.* 2012). Recent studies suggest that environment-driven community assembly may become more important under stressful environmental conditions (Chase 2007; Jiang & Patel 2008; Lepori & Malmqvist 2009), whereas dispersal filtering may become more prevalent under benign conditions (Myers & Harms 2009; Germain *et al.* 2013). In existing communities, species interactions may enforce both types of filtering by competitive displacement of subordinates towards peripheral ends of environmental gradients (Wisheu & Keddy 1992), narrowing species' realized niche ranges (Hutchinson 1957; Pickett & Bazzaz 1978; Silvertown *et al.* 1999), or by preventing establishment of later arriving species ('priority effects'), especially in more productive environments (Chase 2010; Kardol *et al.* 2013). In dynamic habitats that are prone to natural disturbance regimes, it is particularly unclear whether environmental filtering or dispersal filtering dominates, or how the two interact in community assembly (Lepori & Malmqvist 2009; Myers & Harms 2009; Brederveld *et al.* 2011). Information on the relative importance of both filters under these circumstances is however urgent, as natural disturbance regimes are an intrinsic feature of many highly diverse and ecologically important habitats that are increasingly disrupted by human interventions across the globe (Mack & D'Antonio 1998; Shea *et al.* 2004; Turner 2010).

Riparian zones along streams provide a useful model system to study determinants of species distribution patterns within naturally occurring species-rich, dynamic habitats. Flooding-related disturbances instigate community re-assembly and exert strong controls on species recruitment (Chapter 3; Garssen *et al.* 2015), affecting subsequent competitive interactions among species (Wilson & Keddy 1986; Kotowski *et al.* 2010). These dynamics coincide with a strong hydrological gradient from the channel to the upland, together generating gradients in the vegetation that are commonly explained by species niche separation (more specifically, their

'hydrological niches'; Silvertown *et al.* 1999) as induced by partitioning of space and water as a resource (Silvertown *et al.* 2015). In order for environmental filtering to serve as the basis for these gradients, ample arrival of the relevant species should take place across the entire gradient. Dispersal studies, however, have shown that arrival of plant propagules (either seeds or vegetative fragments) along stream riparian zones is controlled strongly by spatially and temporally highly variable flooding events (Boedeltje *et al.* 2004; Moggridge *et al.* 2009; Chapter 2), which may lead to priority effects in riparian community assembly (J.M. Sarneel *et al.*, unpublished data), suggesting an important role for dispersal filtering as well.

Thus, recent advances in dispersal research that reveal strong spatiotemporal patterns in propagule arrival and dispersal limitation (Nathan & Muller-Landau 2000; Spiegel & Nathan 2007; Puerta-Piñero *et al.* 2013; Sarneel *et al.* 2014a) challenge the long-held view that vegetation patterns and species gradients are principally driven by the environmental conditions and species interactions that limit (or promote) species' growth. This not only applies to riparian zones, but also to many other zoned ecosystems where spatiotemporal patterns in propagule arrival exist, e.g. tidal marshes (Rand 2000), successional woodland gradients (Brunet *et al.* 2000) and mountainous forests (Kessler 2000). To what extent either environmental or dispersal filtering determines community assembly and consequent biodiversity development in such systems remains unknown, and may even be subject to change due to increased dispersal limitation (Soons & Ozinga 2005; Ozinga *et al.* 2009; Brederveld *et al.* 2011). It is however critical to know the relative contributions of these filters for the design of effective conservation and restoration strategies: When environmental filtering dominates, measures should seek to improve or maintain proper local environmental conditions (Roelofs *et al.* 2002; Jähnig *et al.* 2009; Lamers *et al.* 2015) but when dispersal filtering dominates, it is important to protect nearby source populations and secure dispersal pathways (Soons *et al.* 2005; Verhoeven *et al.* 2008; Brederveld *et al.* 2011).

Here, we aimed to elucidate the relative importance of the dispersal filter *versus* the environmental filter for stream riparian vegetation in order to gain a mechanistic understanding of community assembly for a naturally dynamic system with strong gradients in environmental conditions and propagule arrival. Specifically, we investigated seed arrival and subsequent environmental filtering along the riparian hydrological gradient and evaluated how hydrology mediates both types of filtering. By studying these processes in riparian zones that were excavated to bare sand during restoration activities, it was possible to relate patterns in initial seed arrival to adult distribution patterns. At these sites, we simultaneously carried out field experiments to quantify seed germination, seedling survival, and seedling growth across the riparian zones, independently of seed arrival. In this way, we were able to disentangle

the relative contributions of seed arrival (dispersal filter) and local seed germination, seedling survival and growth (environmental filter) to the distribution of adult plants and consequent patterns in early successional vegetation and biodiversity.

MATERIAL AND METHODS

We quantified the relative contributions to community assembly and vegetation pattern development in early successional communities of the following individual, subsequent steps in plant recruitment: seed arrival, seed germination, seedling survival and seedling growth. We measured natural seed arrival patterns of aquatic and riparian plant species across riparian zones at three restored lowland streams in the Netherlands. Simultaneously, for 17 riparian plant species common to north-western Europe, we measured patterns in germination, seedling survival and seedling growth by introducing their seeds and seedlings along these gradients. For overlapping species, patterns in seed arrival (dispersal filter) and patterns in germination, seedling survival and seedling growth (environmental filter) were analysed considering their relative contributions to plant species distribution in the natural developing vegetation 1 and 2 years after restoration.

Study system

Riparian zones form the dynamic transition zones between aquatic and terrestrial environments, encompassing the area between a stream's low and high water marks (Naiman & Décamps 1997). Along streams and rivers, riparian zones are prone to frequent natural flooding disturbances and are characterized by a strong environmental moisture gradient, generating a high spatial and temporal heterogeneity, which promotes a high biodiversity (Gregory *et al.* 1991; Naiman & Décamps 1997; Ward 1998). Lowland streams generally flow through gently sloping terrain (0-5‰ slope) and have low flow velocities (0.05-0.6 m s⁻¹) with discharge patterns and flood events tightly linked to precipitation (Verdonschot & Nijboer 2002).

In the Netherlands, the distribution of lowland streams is restricted to the Pleistocene areas in the central, eastern and southern parts of the country, located directly upstream of the Rhine-Meuse delta (De Vries 1976), with a soil surface built up by Aeolian sand deposits. To allow for water table and flow regulation, almost all streams in the area have been channelized in the past century. This has led to the degradation and disappearance of many of the associated riparian wetlands that previously fulfilled important corridor functions for aquatic and riparian species. These habitats and corridors have therefore become highly scattered and fragmented in the Netherlands, as well as many other regions across the globe (Petts 1988; Poff *et al.* 1997; Malmqvist & Rundle 2002; Baattrup-Pedersen *et al.* 2005; Nilsson *et al.* 2005). Increased awareness of high biodiversity losses in lowland streams and their

riparian zones have promoted measures seeking to restore a more natural hydrology and morphology for streams and riparian zones (Verdonschot & Nijboer 2002; Jähnig *et al.* 2010; Brederveld *et al.* 2011).

We studied early successional community assembly of riparian vegetation along three lowland streams in the Netherlands: the Hagmolenbeek (HM), Hooge Raam (HR) and Kleine Aa (KA) (52°13'0.33" N, 6°43'16.88" E; 51°42'57.65" N, 5°42'9.25" E; and 51°35'39.92" N, 5°16'38.71" E respectively). Restoration measures took place along 0.8-2 km stretches of stream between 2009 and 2011. Morphological changes by the restoration activities involved raising the stream bed, narrowing the channel, and excavating the riparian zones down to bare sand, thereby creating wider riparian zones with more gradual slopes. More information on the research locations is presented in Appendix A3.1 (Chapter 3).

Field experimental set-up

To study the plant recruitment steps along the entire hydrological gradient, three replicate transects of five plots were laid out for each stream perpendicular to the stream channel (Fig. 4.1). At each plot, we monitored the natural seed rain (see below), recruitment of introduced seeds and seedlings (see below), and natural vegetation development. Plot size was approximately 0.3 m perpendicular to the stream, and 4.0 m parallel to the stream channel. Horizontal distances between plots were approximately 0.5, 1.0, 3.0 and 5.0 m (from low to high elevation), and distances between replicate transects were 20-25 m (the maximal distance in the available area). For monitoring the natural vegetation development, species percent cover was registered in permanent quadrants of 25 x 50 cm in July or August, 1 and 2 years after restoration. Hydrological conditions (water tables and surface water levels) were registered hourly at each plot using pressure transducers (Schlumberger Water Services, Delft, the Netherlands; Keller Meettechniek B.V., Reeuwijk, the Netherlands) in water level gauges and 1-2 m deep piezometers (Fig. 4.2), with average values during the experimental periods used for further analyses. We determined the soil parameters organic matter content, particle size distribution and nutrient availability (extractable N and P) by analysing samples of three combined soil cores (4 cm diameter, 10 cm depth) per plot in May 2012, as described in Appendix A3.2 (Chapter 3).

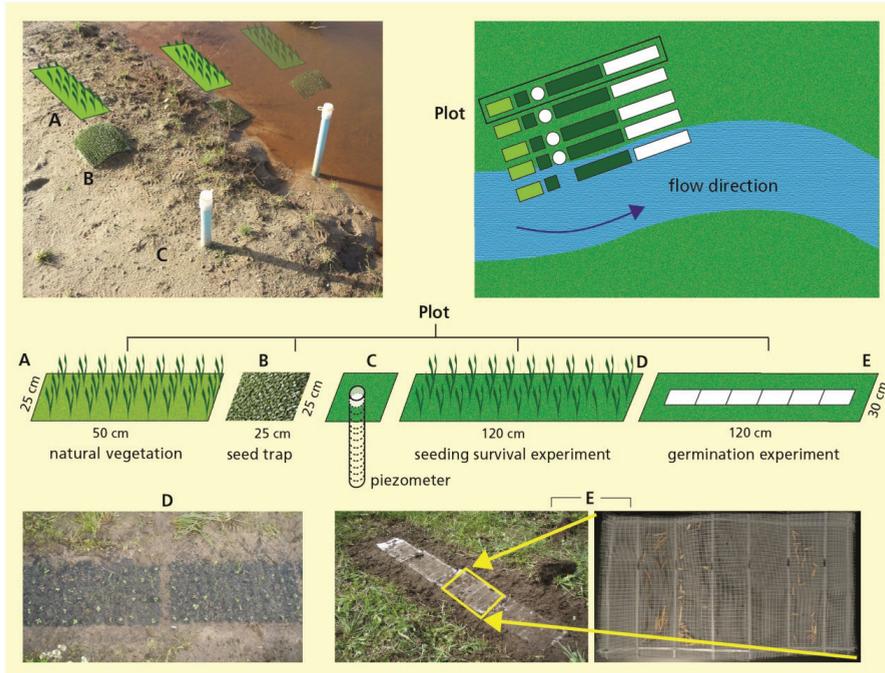


Figure 4.1. Overview of the experimental set-up in the field. Three replicate transects were laid out up stream, each transect consisting of one in-stream plot and four plots at increasing elevations along the riparian gradient. At each plot, we monitored the naturally developing vegetation and the initial seed rain, and we carried out two experiments—a germination experiment, with introduced seeds in mesh bags; and a seedling survival and growth experiment with introduced seedlings. Piezometers were installed to monitor phreatic water levels at each plot.

Natural seed rain

To monitor the natural seed rain, seed traps — i.e. 25 x 25 cm artificial turf mats (Astroturf) with 1.5 cm bristles and ca. 8 bristles per cm² (cf. Goodson *et al.* 2003) — were pinned to the ground in each plot shortly after restoration (December 2010 at HM, May 2011 at HR and October 2011 at KA). All traps were replaced by new ones in April and October in the first year after seed trap placement to analyse seasonal differences in seed arrival. After retrieval from the field, seed traps were stored in plastic bags at 4°C in the dark before further analysis. Processing the stored seed traps involved extracting all deposited material by flushing the seed traps with water, and wet-sieving the deposited material with three sieves of 2.0, 0.5 and 0.1 mm to remove fine silt and clay, and group similarly sized seeds together. Subsequently, the seeds of all Haggmolenbeek seed traps were physically extracted by drying the samples at 70°C for 48 hours, extracting seeds by hand using dissecting microscopes, and identifying

seeds to the species level using an identification guide (Cappers *et al.* 2006). Because this time-consuming method limited the number of seed traps that could be analysed, we switched to seedling emergence trials for seed traps of the remaining sites (*cf.* Boedeltje *et al.* 2002; Gurnell *et al.* 2006, 2008). In these trials, the wet-sieved seed trap content was spread out over waterlogged trays (60 x 40 x 10 cm) filled with sand, in a greenhouse under conditions of 15:9 h light:dark period (air temperature 25:15 °C) with 400W overhead plant growth lights (*cf.* Boedeltje *et al.* 2002). Emerging seedlings were removed weekly to avoid overcrowding and were identified to the species level according to van der Meijden (2005). Trays were kept waterlogged for ten weeks, subsequently allowed to dry slowly for four weeks and then were submerged (5 cm water layer above sediment) for four weeks to provide optimal germination conditions for as many species as possible. Similar amounts of species were detected with both methodologies (physical extraction and seedling emergence). The total number of seeds detected was higher for physical extraction. However, this was largely caused by seeds of only three highly abundant species, more likely reflecting differences between research locations than differences between methods (Appendix A4.1). Overall, we have no reason to expect that the different methods affected our results.

Field experiments on germination, seedling survival and growth

Two experiments were performed with 17 common riparian plant species: a germination experiment with introduced seeds, and a seedling survival and growth experiment with introduced seedlings. Plant species were selected to be representative for the entire range of hydrological conditions along the riparian gradient, as indicated by their Ellenberg F-values. The species used ranged from those with relatively dry moisture optima (Ellenberg F 4) to those with shallow water habitats (Ellenberg F 10) (Ellenberg 1988, adjusted by Hill *et al.* 1999). The full list of species is provided in Table 3.1 (Chapter 3). Seeds of all species were purchased from commercial suppliers of wild plant seeds. These suppliers either collect seeds from natural wild populations, or safeguard a close connection to wild populations by minimizing the amount of produced generations from their wild origin (mostly being separated by only one generation). All seeds were stored at 4°C in the dark prior to use.

For the germination experiment, two sets of mesh bags (mesh size 680 µm, thread diameter 150 µm, and parallel compartments of 8 × 4 cm to group seeds of single species; Fig. 4.2) containing 20 seeds per species per bag were pinned to the sediment in each plot. After 2 and 3 months (to evaluate possible effects of environmental fluctuations over time) the mesh bags were taken to the laboratory to score germination. Germination during the two periods was pooled for further analysis, as few differences were observed between the periods. A control experiment indicated that the use of mesh bags slightly decreased germination, but did not influence patterns

in germination along the riparian gradient (Chapter 3). The germination experiment was performed between May and August 2012 (and for nine species at HM and HR in 2011).

For the seedling survival and growth experiment, 10 seedlings per species (three- to four-week-old, grown from the seeds in a greenhouse facility) were transplanted to each plot in the field. Within each plot, seedlings were randomly arranged in a rectangle of 120 × 20 cm (Fig. 4.1), resulting in a distance of 3.5 cm between individual seedlings. Seedling survival was scored after 2 weeks and 1, 2 and 3 months. The biomass of living shoots was measured after 3 months (above-ground weight after drying at 70°C for 48 h). More details on both experiments are given in Chapter 3.

Data analysis of species distribution patterns

We analysed all species distribution patterns in relation to the water level (vertical distance from the plot surface to the water table), as this environmental variable has previously been shown to be by far the dominant variable determining germination and seedling survival and growth in lowland riparian zones (Chapter 3). In our analyses of initial patterns in seed arrival, we excluded seeds of the few species that had already established as adults in the period of seed rain monitoring. Furthermore, we excluded all species that arrived or became established in only a single plot. For all remaining seed species, we used the seed trap data to model patterns in initial seed arrival with water level as explanatory variable. For the species within this dataset that were also used in the experiments, patterns in germination, seedling survival and seedling growth were similarly modelled with water level as explanatory variable.

For each colonization process (seed arrival, germination, seedling survival, growth), individual species responses showed non-linear patterns along the hydrological gradient. Since non-linear patterns are not supported in regular generalized linear mixed models (GLMM), a smoothing function (spline) on the predictor variable was used to model these responses. We used Bayesian P-splines (Marx & Eilers 1998; Lang & Brezger 2004), and fitted these in GLMMs with the R package INLA (Rue *et al.* 2014), as further detailed in Appendix A3.3 (Chapter 3). In these models, we used logistic links with a negative binomial (seed arrival) or beta-binomial error distribution (germination and seedling survival), or the identity link with a normal error distribution (for log-transformed seedling growth). The beta-binomial instead of the binomial error distribution was used to account for overdispersion in the data. Transects were included as random effects (intercept) in all models. Streams were not included as additional random effects, because exploratory analyses confirmed that we captured the largest part of variability imposed by the multilevel design by including transects (which is a finer grouping level than streams),

while obtaining more stable results.

After modelling all species responses in relation to the hydrological gradient, we used the model predictions of species responses along the hydrological gradient as explanatory variables ('process variables' from here) in binomial GLMMs (R package lme4; Bates *et al.* 2014) to explain species presence in the vegetation 1 and 2 years after restoration. In this analysis, we again used transects as random effects (intercept). In tiered forward selections (Jamil *et al.* 2012), we tested the significance of additional random effects of species (intercept and slope), followed by the selection of process variables as fixed effects. Finally, we tested for significance of additional effects of abiotic variables (all log-transformed except water level), by first selecting additional random effects of species (slope), and then abiotic variables as fixed effects. Significant model improvement by addition of a variable was defined as a decrease in Akaike's Information Criterion (AIC) by at least 2 units (Burnham & Anderson 2002). The reported model statistics for analyses on species distribution patterns involve the marginal R^2 , representing the explained variance by the fixed effects only, and Wald p-values.

Data analysis of community patterns

To analyse patterns in community composition along the riparian gradient, we calculated a weighted Ellenberg F-value (Diekmann 2003), Shannon diversity index (Magurran 2004) and total species richness per plot, for each process and for the established vegetation. We applied abundance weighting, because this is more reliable than community weighting on presence-absence data for species-poor habitats, as was the case for several of our plots (Diekmann 1995; Ellenberg 1992 in Dieckmann 2003). We investigated whether water level affected patterns in weighted Ellenberg F-values, Shannon diversity and species richness along the riparian gradient using linear mixed models (LMM) and GLMMs with transects as random effects (intercept) and an exponential or quadratic term for water level as explanatory variable.

The effect of the colonization processes on weighted Ellenberg F-value, Shannon diversity and species richness of the vegetation 1 and 2 years after restoration was also tested using (G)LMMs, with transects as random effects (intercept). Contrary to the analyses on species patterns, where we used process variables predicted by water level, we here used the observed community values as explanatory process variables, because community-weighting already reduces variability by averaging among species. Next to the separate effect of each process on community patterns in the vegetation, a tiered forward selection was carried out based on AIC improvement as described above (without additional selection of species as random effects). A subset of the data of 35 plots was used in this forward selection, as missing values in any process were not allowed for model comparison. For all analyses on community

patterns, response and explanatory variables were log-transformed to improve normality when necessary (based on the Shapiro-Wilcoxon test, or when observed values were close to zero), using the R package lme4 (Bates *et al.* 2014) for modelling. Model statistics of analyses on community patterns present the marginal R^2 with p-values based on likelihood ratio tests. All analysis were performed in R 3.1.1 (R Core Team 2014), using ggplot2 for graphs (Wickham 2009).

RESULTS

Species distribution patterns

We observed initial seed arrival on the bare sand of the re-excavated streams and riparian zones for a total of 79 species in the first year after restoration (for a complete species list, see Appendix A4.2). Seeds of 58 species were detected in more than one seed trap and exhibited clear patterns in seed arrival along the hydrological gradient. Patterns in initial seed arrival were often reflected in species distribution patterns in the establishing vegetation (for a visual comparison, see Appendix A4.3). Model predictions of initial seed arrival along the hydrological gradient significantly explained species presence in the vegetation (for 19 and 28 of the subset of 58 species, 1 and 2 years after restoration respectively), which was even more significant for species distributions 2 years after restoration (1 year: $R^2 = 0.20$, $p = 0.019$; 2 years: $R^2 = 0.22$, $p = 0.005$). After having accounted for seed arrival in a tiered forward selection, additional effects of soil organic matter content and either N availability or P availability were selected as significantly explaining species presence in the vegetation 1 and 2 years after restoration, but additional explained variance was low (Table A4.4.1 in Appendix A4.4).

For four species (*Glyceria maxima*, *Lycopus europaeus*, *Myosotis scorpioides* and *Ranunculus flammula*), we obtained sufficient data on all colonization processes (i.e. seed arrival in at least two plots, experiments on germination, seedling survival and seedling growth, and presence in the vegetation in at least two plots) to enable a relative comparison of the dispersal filter (patterns in initial seed arrival) *versus* the environmental filter (patterns in germination, seedling survival, and seedling growth) in determining species distribution patterns. Strikingly, patterns in seed arrival showed the strongest resemblance with species distribution patterns along the hydrological gradient (Fig. 4.2). Model predictions of seed arrival explained most of the variance of species presence in the vegetation 1 year after restoration. Following seed arrival, also germination and seedling survival were selected as significant explanatory variables, although their combined impact explained less variation than seed arrival (Table 4.1). Two years after restoration, the result of the forward selection was comparable to that after 1 year, but with less explained variance by seed arrival and germination, and an

increase in explained variance by seedling survival. Thus, the investigated processes explained species presence in the vegetation, with patterns in seed arrival forming a strong dispersal filter, and germination and seedling survival being the most significant environmental filters. None of the abiotic variables further improved the models.

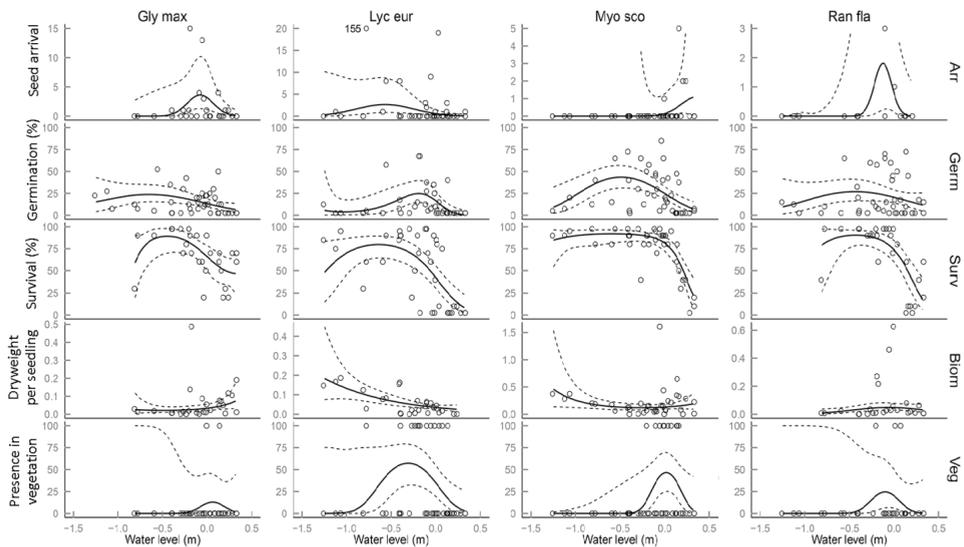


Figure 4.2. Species-specific patterns along the riparian gradient in seed arrival, germination, seedling survival, seedling growth and presence in the vegetation 1 year after restoration (from upper to lower panel respectively), with negative water level values indicating water levels below the soil surface and positive values indicating water levels above the soil surface (flooding). Best model fits to the field data (open circles) are visualized by continuous lines, with 95% credible intervals of the modeled relationships displayed by dotted lines.

Table 4.1. Tiered forward selections of explanatory variables in binomial GLMMs explaining species presence in the vegetation 1 and 2 years after restoration, with the variance explained (R^2) and model fits (AIC) for each model. Selection of random effects (between parentheses) preceded the selection of fixed effects, with '(1 | ...)' indicating random intercepts and '(1 + variable | ...)' random slopes. Transects, species, seed arrival (Arr), germination (Germ), seedling survival (Surv), and seedling growth (Biom) were added in tier 1 and 2. From tier 3 onwards (below the dashed line) additional effects of the abiotic variables water level (WL), soil organic matter content (OM), soil grain size (Grain), and soil extractable P (P), and N (N) were tested on the best model of the preceding tier. The best model in each tier (with >2 units AIC decrease for addition of a variable) is underlined.

1 year after restoration			2 years after restoration		
Tier	Effects	R ² AIC	Tier	Effects	R ² AIC
	<u>(1 Transects)</u>	148.4		(1 Transects)	147.1
1 + (1 Species)	149.2	1 + (1 Species)	141.4
1 + (1 + Arr Species)	149.7	1 + (1 + Arr Species)	139.7
1 + (1 + Germ Species)	148.3	1	<u>.... + (1 + Germ Species)</u>	136.8
1 + (1 + Surv Species)	152.0	1 + (1 + Surv Species)	141.6
1 + (1 + Biom Species)	153.9	1 + (1 + Biom Species)	144.6
2	+ Arr	0.35 143.0	1 + (1 + Germ + Arr Species)	138.5
2	+ Germ	0.02 149.0	1 + (1 + Germ + Surv Species)	141.7
2	+ Surv	0.00 150.2	1 + (1 + Germ + Biom Species)	141.9
2	+ Biom	0.00 150.2	2	+ Germ	0.00 138.7
2	+ Arr + Germ	0.50 139.2	2	+ Germ + Arr	0.15 136.3
2	+ Arr + Surv	0.35 144.7	2	+ Germ + Surv	0.06 136.7
2	+ Arr + Biom	0.35 144.6	2	+ Germ + Biom	0.04 139.8
2	<u>+ Arr + Germ + Surv</u>	<u>0.65 133.6</u>	2	<u>+ Germ + Arr + Surv</u>	<u>0.65 130.6</u>
2	+ Arr + Germ + Biom	0.51 140.3	2	+ Germ + Arr + Biom	0.28 136.6
2	+ Arr + Germ + Surv + Biom	0.68 134.5	2	+ Germ + Arr + Surv + Biom	0.55 131.1
3 + (1 Species)	133.7	3	(.... + WL Species)	134.2
3 + (1 + WL Species)	135.7	3	(.... + Gr Species)	136.2
3 + (1 + Gr Species)	139.7	3	(.... + OM Species)	136.0
3 + (1 + OM Species)	139.7	3	(.... + P Species)	133.7
3 + (1 + P Species)	139.7	3	(.... + N Species)	134.7
3 + (1 + N Species)	138.7	3	(.... + N Species)	134.7
4 + WL	0.73 134.6	4 + WL	0.63 132.2
4 + Gr	0.61 134.5	4 + Gr	0.66 129.6
4 + OM	0.64 135.5	4 + OM	0.69 129.0
4 + P	0.69 133.4	4 + P	0.43 131.6
4 + N	0.65 132.9	4 + N	0.65 131.0

Community patterns

Analyses at the community level showed that strong pattern formation occurred in the establishing vegetation already 1 year after restoration. Species for which adults are associated with wet habitats (high Ellenberg F-values) dominated the vegetation at the wet end of the hydrological gradient, while species with lower Ellenberg F-values dominated the dry end. This resulted in a strong, exponential relation between weighted Ellenberg F-values of the vegetation and water level along the riparian gradient (Fig. 4.3, upper panel). Interestingly, this pattern reflects both dispersal filtering (patterns in seed arrival) and environmental filtering (patterns in seed germination, seedling survival, and seedling growth), which all showed comparable exponential relations along the riparian gradient (Fig. 4.3). Weighted Ellenberg F-values of the vegetation were significantly explained by all four investigated processes in linear mixed models, with high explained variance for seedling growth, seedling survival and seed arrival, and lower explained variance for germination (Fig. 4.3, upper arrows). For the vegetation 2 years after restoration, the results were comparable (Appendix A4.5). In a forward selection, the best model included seedling growth and seed arrival as fixed effects for both years. Some abiotic variables explained additional variance, most importantly soil organic matter content (1 year after restoration) and grain size (2 years after restoration), but also water level and soil N and P availability (Table A4.4.2 in Appendix A4.4).

The Shannon diversity of the vegetation showed sharp decreases both at the wetter and drier ends of the gradient. This pattern along the hydrological gradient was significantly explained by environmental filtering (particularly by seedling survival), but not by dispersal filtering (Fig. 4.3 lower arrows; Appendix A4.5). In a forward selection, seedling survival led to the best model improvement for both years, with additional selection of seedling growth, only for 1 year after restoration. Abiotic variables did not result in any additional model improvements (Table A4.4.3 in Appendix A4.4).

However, when considering species numbers instead of Shannon diversity (thus excluding species' relative abundances), we obtained different results, with changes in plant species numbers along the riparian gradient significantly explained by patterns in seed arrival ($R^2 = 0.19$, $p = 0.004$), germination ($R^2 = 0.41$, $p < 0.001$), and seedling survival ($R^2 = 0.67$, $p < 0.001$) (Fig. 4.4). In this case, forward selection resulted in the selection of both seedling survival and seed arrival, with further model improvement by addition of water level (Table A4.4.4 in Appendix A4.4). Seed arrival thus contributed to the development of biodiversity patterns, but was only significant with respect to species richness and not for Shannon diversity. Overall, both diversity metrics indicated that environmental filtering at the germination and seedling stage was most significant in determining riparian plant diversity.

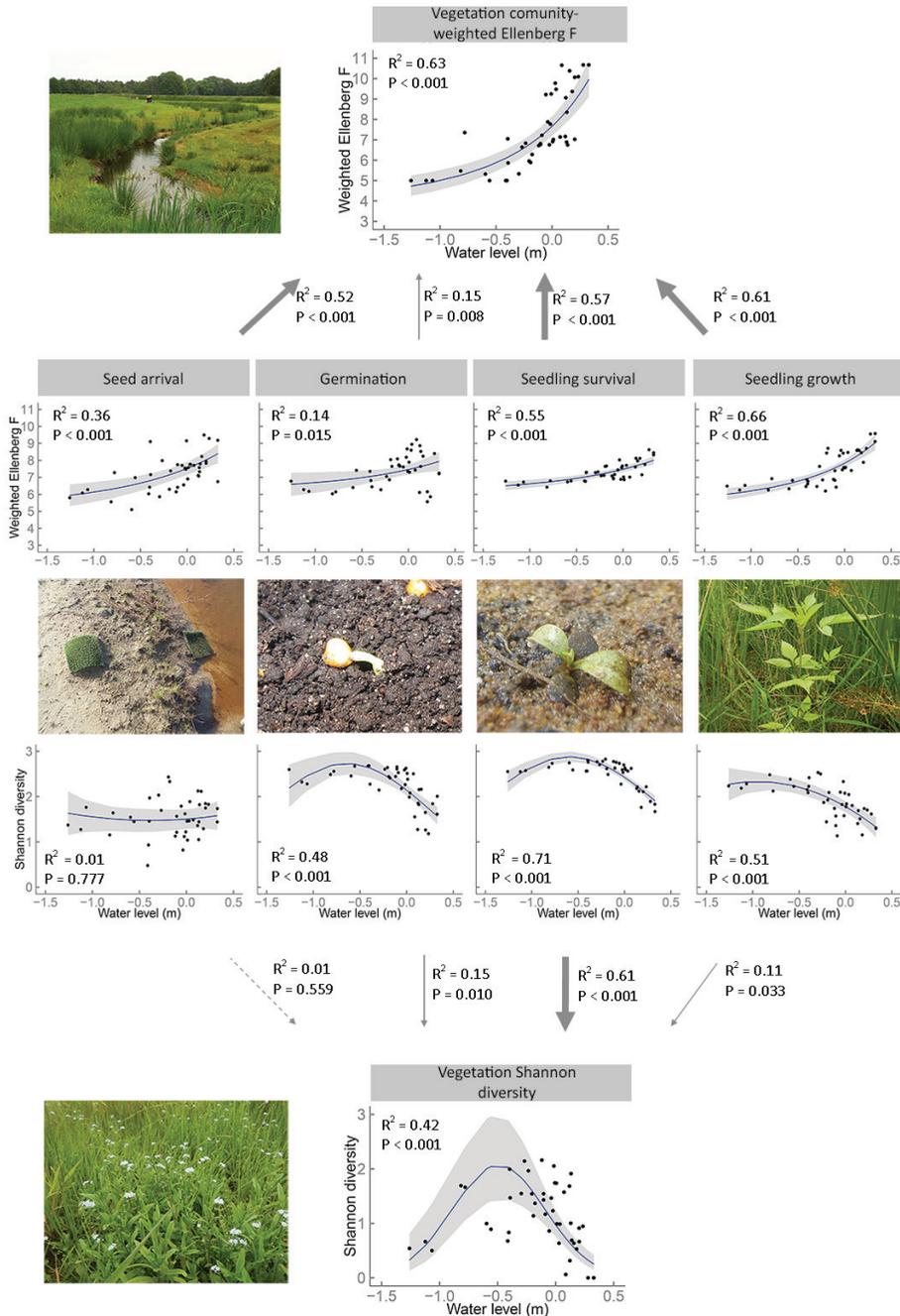


Figure 4.3. Patterns in weighted Ellenberg F-values (upper five graphs) and Shannon diversity (lower five graphs) of the different communities (seeds, seedlings and the vegetation 1 year after restoration) along the hydrological gradient, as shaped by the processes of seed arrival, germination, seedling survival and seedling growth. Negative water level values indicate water levels below the soil surface and positive values indicate

water levels above the soil surface (flooding). Blue lines represent best model fits of LMMs to the field data (dots), with exponential relationships for weighted Ellenberg F-values and quadratic relationships for Shannon diversity. 95% confidence intervals (based on fixed effects only) are indicated by the grey ribbon, with model statistics in the upper or lower left corner, using transects as random effects (intercept) in all models. Linear relations between the processes and the vegetation were tested using LMMs with transects as a random effect (intercept); model statistics are shown next to the grey arrows (thickness of the arrows proportionally to the R^2 value of the relation).

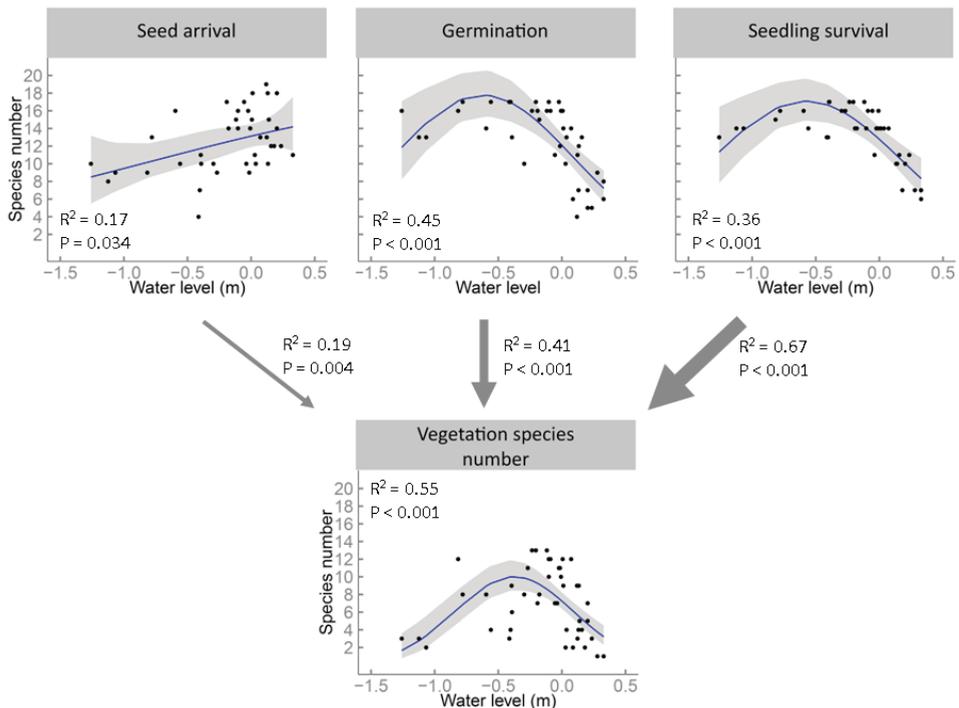


Figure 4.4. Patterns in species numbers of the different communities (seeds, seedlings and vegetation 1 year after restoration) along the hydrological gradient as shaped by the processes of seed arrival, germination and seedling survival. Negative water level values indicate water levels below the soil surface and positive values indicate water levels above the soil surface (flooding). Blue lines represent best model fits of GLMMs to the field data (dots), with quadratic relationships. 95% confidence intervals (based on fixed effects only) are indicated by the grey ribbon, with model statistics in the upper or lower left corner, using transects as random effects (intercept) in all models. Linear relations between the processes and the vegetation were tested using GLMMs with transects as random effect (intercept); model statistics are shown next to the grey arrows (thickness of the arrows proportionally to the R^2 value of the relation).

DISCUSSION

Dispersal filtering

Species-specific patterns in initial seed arrival exerted a strong influence on species distribution patterns along the riparian gradients of the restored streams. These strong relations between patterns in arrival and in establishment suggest that dispersal filtering dominated at least the early distribution patterns of plant species, and that environmental filtering was of secondary importance. This was a surprising result, as steep moisture gradients and flooding disturbances may make large parts of riparian zones a harsh environment for many plant species, which is generally known to stimulate environmental filtering (Keddy & Ellis 1985; Squirres & van der Valk 1992; Hölzel & Otte 2003; Van Eck *et al.* 2004; Kotowski *et al.* 2010; Garsen *et al.* 2014, 2015; Chapter 3). The strong role of dispersal filtering in our study could partly be explained by the low interspecific competition that prevailed in the first years after restoration activities. In further developed (closed) vegetation, species interactions are likely to further narrow down niche ranges (Pickett & Bazzaz 1978; Silvertown *et al.* 1999, 2015), thereby enforcing the effect of environmental filtering.

Yet, natural disturbances that set back succession (and create empty patches) and therewith reduce competition are a characteristic feature of natural riparian zones, suggesting that dispersal filtering retains an important role also at natural sites with more developed vegetation – although this role is likely to depend on the frequency and level of disturbance. Indeed, strong indications for dispersal filtering have been reported in fully developed riparian vegetation: Species richness of riparian vegetation significantly increased with the number of stranded seeds or seed mimics (Andersson *et al.* 2000) or with seed concentrations in the water column (Merritt & Wohl 2006). This concurs with the finding that many plant communities are seed-limited (Clark *et al.* 2007; Myers & Harms 2009; Aicher *et al.* 2011), and that dispersal limitation of particularly water-dispersed species may restrain species diversity (Merritt *et al.* 2010), inhibits biodiversity recovery after restoration (Brederveld *et al.* 2011), and even forms a major cause to species declines in north-western Europe (Ozinga *et al.* 2009). These findings highlight the fact that in dynamic habitats like stream riparian zones, dispersal filtering (or dispersal limitation) may play a very important role in community assembly.

The primary role of dispersal filtering in determining plant species distributions was less reflected by community patterns in the vegetation. While patterns in vegetation weighted Ellenberg F-values and species richness could in part be explained by seed arrival, patterns in vegetation Shannon diversity could not. All three vegetation characteristics showed a more environment-driven pattern (although dispersal filtering played a comparably strong role for weighted Ellenberg F-values)

along the hydrological gradient, strongly reflecting environmental filtering during the seedling survival and growth stages.

Still, not only environmental filtering induced pattern formation in the vegetation community across the gradient. Strikingly, patterns in seed arrival already foreshadowed a pattern in the vegetation, with species with adult optima at wetter conditions dominating seed arrival at low elevations along the riparian gradient, and species with drier optima dominating the arrived seed community higher up. Such patterns of seed dispersal to sites suitable for establishment and growth are generally known from highly specialized animal-mediated dispersal syndromes, e.g. ants or frugivorous birds that disperse seeds to optimal sites for establishment (Wenny 2001; Spiegel & Nathan 2007). Very few studies have suggested that a comparable phenomenon may be relevant for riparian vegetation. Seiwa *et al.* (2008) showed that seeds of riparian willows were disproportionally dispersed to discrete and predictable microsites favourable for their establishment, as influenced by the seed's cottony hairs that promote flotation. Merritt & Wohl (2002) also discussed directed dispersal for riparian plant species in relation to the systematic delivery of seeds to specific types of fluvial environments in a flume study. Adaptations promoting seed flotation (including air-sacs, 'cork-like' tissues or water-repellent outer layers; van der Pijl 1972; Nilsson *et al.* 2010) allow many riparian plant seeds to travel large distances by water, but may also have evolved to promote deposition around the water line in riparian zones – although at this point, this remains speculative. While the exact mechanisms behind these patterns provide an interesting avenue for future research, our study clearly demonstrates that species-specific patterns in seed arrival already initiate a gradient in species distributions that one might expect to be generated by environmental filtering solely. This phenomenon may have been overlooked previously for vegetation patterns along riparian gradients, but also along environmental gradients in other ecosystems where interspecific interactions are (temporarily) reduced, for example after restoration activities.

Environmental filtering

Besides dispersal filtering, environmental filtering at the seed germination, seedling survival and growth stages contributed to species distribution patterns and to community patterns across the stream riparian gradient. Although predictors were often intercorrelated (making it difficult to draw conclusions on causal mechanisms), the contribution of environmental filtering to biodiversity patterns (species richness and especially Shannon diversity) was clearly greater than that of dispersal filtering, particularly during the stages of seedling survival and growth. Under flooded conditions, the role of environmental filtering was most apparent. Indeed these conditions yielded the highest diversity of arriving seeds, yet strongly reduced diversity of the vegetation.

These results confirm our earlier findings that flooding along riparian zones drastically inhibits germination, seedling survival and seedling growth, except for those species with higher Ellenberg F-values (Chapter 3), which supports the notion of a strong environmental filtering under harsh environmental conditions (Chase 2007; Lepori & Malmqvist 2009). Dry conditions, at higher elevations along riparian zones, may also cause environmental filtering, by hampering seed imbibition (Evans & Etherington 1990), causing high seedling mortality (Grime & Curtis 1976) and reducing seedling growth (Haugland & Froud-Williams 1999), but these played a less important role to species sorting along the riparian gradients than flooding stress in the present study.

After having accounted for patterns in seed arrival and subsequent germination, survival and growth, purely abiotic variables did not explain additional variance of individual species distribution patterns, nor Shannon diversity of the vegetation community. Only for weighted Ellenberg F-value and species richness of the vegetation, organic matter content, grain size, water level and soil N and P availability explained some additional variance. Soil N and P and water availability (both shortages and surpluses) may significantly influence plant growth and affect competition (Güsewell 2004). High soil organic matter content and a small particle size stimulate the soil water holding capacity (Saxton & Rawls 2006), which may have favoured species with higher moisture requirements (Evans & Etherington 1991). While the role of abiotic variables other than water level in explaining early successional vegetation and diversity patterns was limited, the role of environmental filtering is likely to increase in further developed vegetation. There, interspecific competition is likely to further strengthen species sorting along the riparian gradients (Pickett & Bazzaz 1978; Wisheu & Keddy 1992). Altogether, however, patterns in seed arrival, germination, seedling survival and seedling growth (which were all primarily regulated by water level), almost solely controlled early successional species distribution and community patterns along the riparian gradients.

These results underline the importance of recruitment stages in determining plant species distributions, as early successional developments form a template for all later successional development. In our case, the vegetation patterns that were formed after 1 and 2 years largely resembled vegetation patterns of established (not recently restored) vegetation in the area (Appendix A4.6). This supports the notion that environmental filtering during recruitment already contributes to the development of vegetation patterns and biodiversity, independently of further strengthening of the environmental filtering during later interspecific competition (Keddy & Ellis 1985; Evans & Etherington 1990, 1991; Eriksson & Ehrlén 1992; Kotorová & Lepš 1999; Stampfli & Zeiter 2008; Sarneel *et al.* 2014b).

Implications

The results of our study support the general idea of strong environmental filtering, leading to hydrological niches, determining species coexistence along hydrological gradients (Silvertown *et al.* 1999, 2015). However, our results also demonstrate that dispersal filtering is another important determinant of species distributions and vegetation patterns, at least along early successional riparian gradients. While species interactions during later successional stages are likely to further affect species distributions and vegetation zonation, these interactions operate on the template set during early successional stages – and their importance will depend on the disturbance dynamics of the system. As such, our findings stress the necessity of considering both dispersal filtering and environmental filtering in studies and models on community assembly (Tilman 2004; Gravel *et al.* 2006; Adler *et al.* 2007). In addition, our findings suggest that patterns of seed arrival may play an important role in seemingly deterministic species distributions and biodiversity patterns. To our knowledge, such a role of dispersal underlying gradients in vegetation has not been demonstrated previously, and may be overlooked also in other ecosystems in which natural disturbance regimes and environmental gradients generate high species diversities. This distinction may be important to directing subsequent management and restoration efforts for such dynamic habitats and environmental gradients. Particularly, this warrants more attention to halting the ongoing loss of propagule sources, dispersal vectors and connectivity, which all reduce seed arrival and increase dispersal limitation, thereby affecting not only species distributions but eventually also species survival and the success of conservation and restoration activities (Lindborg & Eriksson 2004; Verhoeven *et al.* 2008; Ozinga *et al.* 2009; Brederveld *et al.* 2011).

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DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.h8p4n>.

Appendix A4.1. Comparison of seed count methods

The seed traps of the HM-site were analysed by physically extracting seeds, while for the seed traps of the HR- and KA-sites a seedling emergence method was used. Similar amounts of species were detected with both seed count methods (Table A4.1.1). Although the number of seeds was higher by physical extraction, this was largely caused by seeds of only three highly abundant species, most likely reflecting differences between research locations rather than differences in seed count methods. Overall, these results suggest that the different seed count methods did not greatly affect the results in our study.

Table A4.1.1. Overview of the number of seeds and species per research location

All species included

Location	Method	Tot nr	Tot nr	Mean nr species	
		species	seeds	+ - sd	Mean nr seeds
HM	Physical extraction	37	12269	13.00 (4.71)	817.93 (696.59)
HR	Seedling emergence	37	931	11.67 (2.38)	62.07 (36.53)
KA	Seedling emergence	42	1838	13.00 (2.54)	181.30 (114.65)

Without three most abundant species

Location	Method	Tot nr	Tot nr	Mean nr species	
		species	seeds	+ - sd	Mean nr seeds
HM	Physical extraction	34	2318	10.53 (4.16)	154.53 (101.16)
HR	Seedling emergence	34	903	10.53 (2.10)	60.20 (36.22)
KA	Seedling emergence	40	1312	11.20 (2.70)	128.90 (80.39)

Appendix A4.2. List of species (seeds and vegetation)

Table A4.2.1. List of species recorded in the seed rain and/or the established vegetation at the three study sites, with the number of plots in which species showed initial seed arrival and became established in the vegetation 1 and 2 years after restoration, followed by their Ellenberg F-values. Species were alphabetically ordered within each of two groups: species that arrived in at least two plots and became established in the vegetation in at least two plots 1 or 2 years after restoration (above the dashed line), and species that showed arrival and/or establishment in fewer plots (below the dashed line). When species identification was uncertain, all possible species were listed and separated by a backslash (with more than three possibilities listed below the table), and Ellenberg F-values were averaged. In case accuracy of species identification differed between observations of seed arrival and presence in the vegetation at the same study site (where most likely this involved the same species), the lower species accuracy was allocated to both observations for analyses on species distribution patterns and for counting the number of occurrences. Nomenclature according to van der Meijden (2005).

Species	Seed arrival (number of plots)	Vegetation year 1 (number of plots)	Vegetation year 2 (number of plots)	Ellenberg F-value	Species	Seed arrival (number of plots)	Vegetation year 1 (number of plots)	Vegetation year 2 (number of plots)	Ellenberg F-value
<i>Alisma plantago-aquatica</i>	25	0	5	10	<i>Crepis capillaris</i>	0	1	4	4
<i>Alnus glutinosa</i>	13	1	6	8	<i>Cynosurus cristatus</i>	0	1	0	5
<i>Betula pendula/pubescens</i>	15	4	1	6	<i>Digitaria ischaemum</i>	1	5	4	4
<i>Bidens frondosa</i>	3	11	13	NA	<i>Echinochloa crus-galli</i>	18	1	0	NA
<i>Callitriche platycarpa/ obtusangula/stagnalis</i>	5	16	10	10.7	<i>Eleocharis acicularis</i>	0	0	1	10
<i>Cerastium glomeratum</i>	3	0	4	5	<i>Elodea canadensis</i>	0	1	2	12
<i>Chenopodium album/polyspermum</i>	15	0	2	5.5	<i>Elodea nuttallii</i>	0	0	2	12
<i>Cirsium arvense</i>	2	1	2	6	<i>Epilobium montanum/ tetragonum</i>	0	2	1	6.5
<i>Conyza canadensis</i>	16	1	5	4	<i>Eupatorium cannabinum</i>	0	0	3	8
<i>Epilobium ciliatum</i>	6	4	3	6	<i>Festuca gigantea</i>	0	0	1	6
<i>Epilobium tetragonum/ ciliatum/ parviflorum</i>	9	4	5	7.3	<i>Festuca pratensis</i>	0	0	3	6
<i>Glyceria fluitans</i>	7	3	4	10	<i>Festuca rubra</i>	0	0	1	5
<i>Glyceria maxima</i>	11	2	2	10	<i>Filipendula ulmaria</i>	2	0	1	8
<i>Gnaphalium luteo-album</i>	6	1	2	7	<i>Galinsoga parviflora</i>	1	0	0	4
<i>Gnaphalium uliginosum</i>	28	10	6	6	<i>Galinsoga quadriradiata</i>	3	0	0	5
<i>Lycopus europaeus</i>	13	13	21	8	<i>Galium palustre</i>	0	2	7	9
<i>Lythrum salicaria</i>	12	1	2	9	<i>Hieracium sp*</i>	1	0	0	4
<i>Mentha aquatica</i>	6	3	10	8	<i>Holcus lanatus</i>	1	1	6	6
<i>Myosotis scorpioides</i>	4	10	11	9	<i>Hypericum sp*</i>	11	0	0	6.8
<i>Persicaria maculosa</i>	13	7	2	6	<i>Hypericum perforatum</i>	11	0	0	4
<i>Phragmites australis</i>	2	1	6	10	<i>Hypochaeris radicata</i>	0	0	1	4
<i>Plantago major ssp major</i>	6	5	5	5	<i>Isolepis setacea</i>	6	0	1	9
<i>Ranunculus flammula</i>	2	3	0	9	<i>Jacobaea aquatica/erucifolia/ vulgaris</i>	2	0	0	5.7
<i>Ranunculus sceleratus</i>	28	2	7	8	<i>Juncus articulatus</i>	0	14	16	9
<i>Rorippa palustris</i>	31	13	4	8	<i>Juncus bufonius</i>	0	17	14	7
<i>Rumex obtusifolius</i>	12	1	4	5	<i>Juncus bulbosus</i>	0	2	0	10
<i>Senecio vulgaris</i>	6	2	2	5	<i>Juncus conglomeratus</i>	0	1	4	7
<i>Sonchus arvensis</i>	2	2	2	6	<i>Juncus effusus</i>	0	17	14	7
<i>Stellaria media</i>	14	0	4	5	<i>Lemna minor</i>	0	0	3	11
<i>Typha latifolia/Sparganium emersum/erectum</i>	5	3	6	10.3	<i>Lemna trisulca</i>	0	0	2	12
<i>Achillea ptarmica</i>	0	1	1	8	<i>Leontodon autumnalis</i>	1	0	0	6
<i>Agrostis capillaris/canina</i>	6	0	0	6	<i>Lolium perenne</i>	0	9	11	5
<i>Agrostis stolonifera</i>	0	12	28	6	<i>Lotus pedunculatus</i>	0	0	4	8
<i>Allium schoenoprasum</i>	1	0	0	6	<i>Lysimachia vulgaris</i>	0	1	1	9
<i>Alopecurus geniculatus</i>	0	2	0	7	<i>Matricaria chamomilla</i>	2	1	1	5
<i>Angelica sylvestris</i>	1	0	0	8	<i>Matricaria discoidea</i>	1	0	0	5
<i>Atriplex patula</i>	1	0	0	5	<i>Mentha aquatica x verticillata</i>	1	0	0	8
<i>Betula pubescens</i>	15	0	0	7	<i>Myosotis laxa ssp cespitosa</i>	0	2	0	9
<i>Bidens tripartita</i>	8	0	0	8	<i>Oenanthe aquatica</i>	2	0	0	10
<i>Capsella bursa-pastoris</i>	9	0	0	5	<i>Persicaria lapathifolia</i>	9	0	1	6
<i>Cardamine sp*</i>	0	2	6	7.3	<i>Persicaria minor</i>	6	0	0	8
<i>Carex pseudocyperus/rostrata</i>	1	0	0	9.5	<i>Persicaria mitis</i>	1	0	0	8
<i>Chenopodium album</i>	10	0	0	5	<i>Phalaris arundinacea</i>	0	4	8	8
<i>Convolvulus sepium</i>	0	1	0	8	<i>Phleum pratense ssp pratense</i>	0	6	9	5
<i>Conyza sumatrensis</i>	1	0	0	NA	<i>Poa annua</i>	0	13	5	5

Table A4.2.1. continued

Species	Seed arrival (number of plots)	Vegetation year 1 (number of plots)	Vegetation year 2 (number of plots)	Ellenberg F-value
<i>Poa trivialis</i>	0	4	11	6
<i>Polygonum aviculare</i>	4	1	0	5
<i>Potamogeton alpinus/crispus/natans</i>	4	0	0	11.7
<i>Potamogeton pusillus</i>	0	0	3	12
<i>Potentilla sp*</i>	4	0	0	5
<i>Potentilla anserina</i>	1	0	0	7
<i>Primula vulgaris</i>	2	0	0	5
<i>Ranunculus flammula/repens/sceleratus</i>	0	2	0	8
<i>Ranunculus peltatus</i>	3	0	0	11
<i>Ranunculus repens</i>	1	12	12	7
<i>Ranunculus repens/sceleratus</i>	0	1	1	7.5
<i>Rumex acetosella</i>	0	1	2	5
<i>Rumex hydrolapathum</i>	1	0	0	10
<i>Sagina procumbens</i>	5	0	0	6
<i>Salix alba</i>	0	1	5	7
<i>Salix caprea/cinerea/reichtardii</i>	0	5	6	7.5
<i>Salix cinerea</i>	1	0	0	8
<i>Salix viminalis</i>	0	0	1	8
<i>Scirpus sylvaticus</i>	1	0	0	8
<i>Solanum nigrum ssp nigrum</i>	6	0	0	5
<i>Sparganium emersum</i>	1	0	2	11
<i>Sparganium emersum/erectum</i>	2	0	0	10.5
<i>Sparganium erectum</i>	6	0	0	10
<i>Spergula arvensis</i>	4	0	0	4
<i>Stellaria holostea</i>	0	0	1	5
<i>Taraxacum officinale</i>	1	9	9	5
<i>Trifolium repens</i>	1	17	16	5
<i>Typha latifolia</i>	0	0	4	10
Unknown seedling 1	0	3	0	NA
Unknown seedling 2	0	2	0	NA
Unknown seedling 3	0	1	0	NA
Unknown seedling 4	0	2	0	NA
Unknown seedling 5	0	3	0	NA
Unknown seedling 6	0	0	5	NA
Unknown seedling 7	0	0	1	NA
Unknown seedling 8	0	3	0	NA
<i>Urtica dioica</i>	7	0	1	6
<i>Veronica catenata</i>	6	0	0	10
<i>Vulpia bromoides</i>	0	0	1	4

*Cardamine sp**: *Cardamine amara/flexuosa/hirsuta/pratensis*

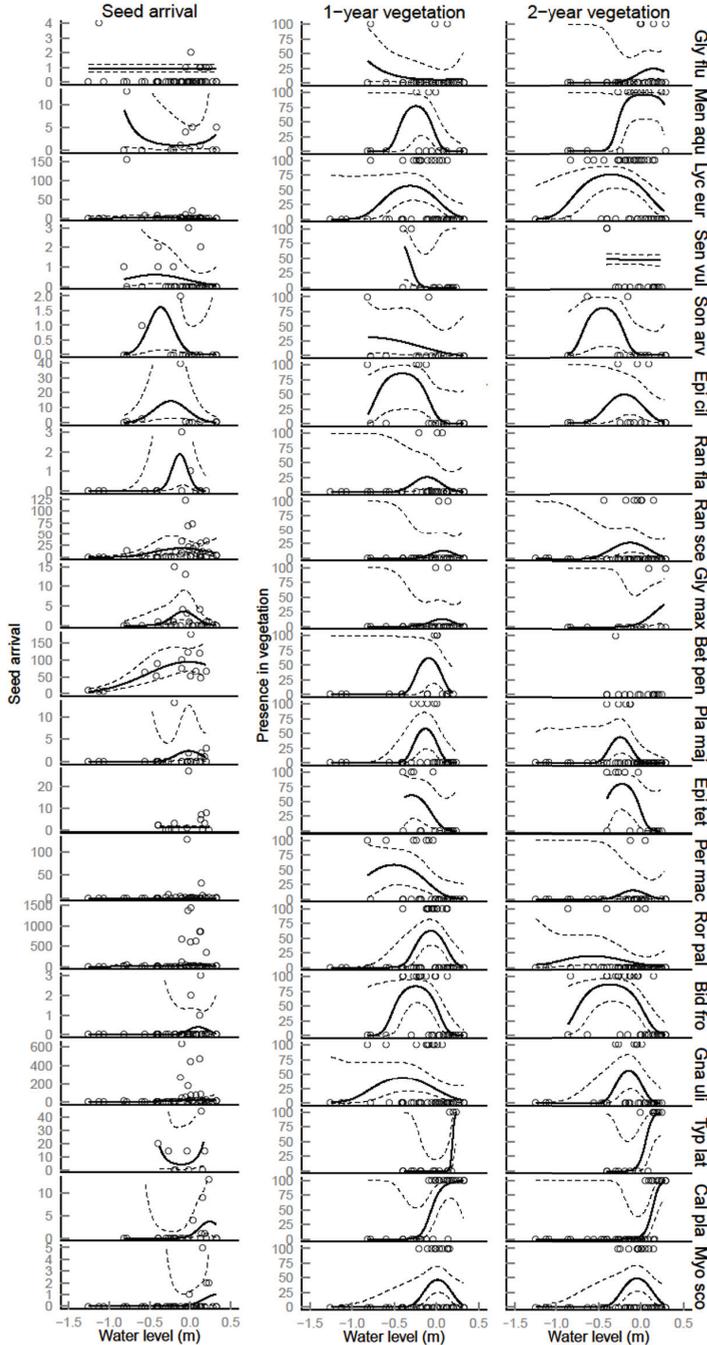
*Hieracium sp**: *Hieracium umbellatum/laevigatum/sabaudum/vulvatum/pilosella*

*Hypericum sp**: *Hypericum elodes/humifusum/maculatum/perforatum/tetrapterum*

*Potentilla sp**: *Potentilla anglica/anserina/argentea/erecta/reptans/sterilis/tabernaemontani*

Appendix A4.3. Species-specific patterns in seed arrival and presence in the vegetation along the riparian gradient

19 species with presence in at least two plots in the vegetation 1 year after restoration



11 species with presence in at least two plots in the vegetation 2 years after restoration

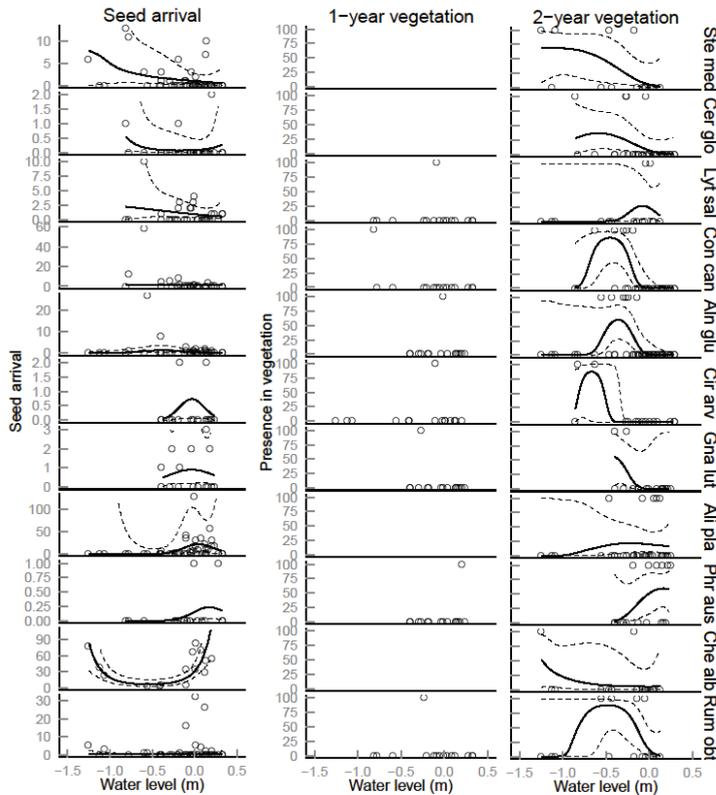


Figure A4.3.1. Species-specific patterns along the riparian gradient in seed arrival, and presence in the vegetation 1 and 2 years after restoration. Negative water level values indicate water levels below the soil surface and positive values indicate water levels above the soil surface (flooding). Continuous lines represent best model fits to the field data (open circles), dotted lines represent 95% credible intervals of the modeled relationships. Species are ordered by their seed arrival optimum (water level at maximal predicted seed arrival) along the hydrological gradient, from optima at most negative water levels (top) to most positive water levels (bottom). Species abbreviations (first three letters of genus and species name) are given on the right. Full names are listed in Appendix A4.2.

Appendix A4.4. Tiered forward selections of explanatory variables in (G)LMMs explaining species distribution and community patterns along the riparian gradient

Tiered forward selections on species distribution patterns with data on arrival and presence only

Table A4.4.1. Tiered forward selections of explanatory variables in binomial GLMMs, explaining species presence in the vegetation 1 and 2 years after restoration (for 19 and 28 species respectively) with the variance explained (R^2) and model fits (AIC) for each model. Selection of random effects (indicated between parentheses) preceded the selection of fixed effects, with '(1 |...)' indicating random intercepts and '(1 + variable |...)' random slopes. Transects, species, and seed arrival (Arr) were added in tier 1 and 2. From tier 3 onwards (below the dashed line) additional effects of the abiotic variables water level (WL), soil organic matter content (OM), soil grain size (Grain), and soil extractable P (P), and N (N) were tested on the best model of the preceding tier. The best model in each tier (with >2 units AIC decrease for addition of a variable) was underlined.

1 year after restoration				2 years after restoration			
Tier	Effects	R^2	AIC	Tier	Effects	R^2	AIC
1	(1 Transects)		558.5	1	(1 Transects)		763.8
1	... + (1 Species)		553.0	1	... + (1 Species)		746.9
1	... + (1 + Arr Species)		539.5	1	... + (1 + Arr Species)		737.5
2	+ Arr	0.20	534.8	2	+ Arr	0.22	728.5
3	(... + WL Species)		534.0	3	(... + WL Species)		719.0
3	(... + Gr Species)		534.9	3	(... + Gr Species)		734.0
3	(... + OM Species)		529.2	3	(... + OM Species)		733.2
3	(... + P Species)		539.6	3	(... + P Species)		714.5
3	(... + N Species)		536.6	3	(... + N Species)		723.7
3	(... + OM + WL Species)		531.2	3	(... + P + WL Species)		714.7
3	(... + OM + Gr Species)		539.1	3	(... + P + Gr Species)		721.1
3	(... + OM + P Species)		532.5	3	(... + P + OM Species)		719.4
3	(... + OM + N Species)		529.0	3	(... + P + N Species)		719.5
4	... + OM	0.18	530.9	4	... + P	0.18	716.5
4	... + OM + WL	0.19	532.7	4	... + P + WL	0.18	718.4
4	... + OM + Gr	0.18	530.5	4	... + P + Gr	0.18	718.0
4	... + OM + P	0.17	532.2	4	... + P + OM	0.19	714.4
4	... + OM + N	0.17	528.2	4	... + P + N	0.19	715.5
4	... + OM + N + WL	0.18	529.9	4	... + P + OM + WL	0.20	716.0
4	... + OM + N + Gr	0.17	529.7	4	... + P + OM + Gr	0.19	716.1
4	... + OM + N + P	0.18	530.5	4	... + P + OM + P	0.19	713.3

Tiered forward selections on weighted Ellenberg F-value of the vegetation

Table A4.4.2. Tiered forward selections of fixed effects in LMMs explaining abundance weighted Ellenberg F-values of the vegetation 1 and 2 years after restoration with the variance explained (R^2) and model fits (AIC) for each model. The effects of seed arrival (Arr), germination (Germ), seedling survival (Surv), and seedling growth (Biom) were tested in tier 1. In tier 2 (below the dashed line), additional effects of the abiotic variables water level (WL), soil organic matter content (OM), soil grain size (Grain), and soil extractable P (P), and N (N) were tested on the best model of tier 1. The best model in each tier (with >2 units AIC decrease for addition of a variable) was underlined. Transects were included as a random effect (intercept) in all models.

1 year after restoration				2 years after restoration			
#	Fixed effects	R^2	AIC	#	Fixed effects	R^2	AIC
1	None	0.00	10.2	1	None	0.00	-5.7
1	Arr	0.62	-20.7	1	Arr	0.46	-27.0
1	Germ	0.07	10.0	1	Germ	0.05	-5.6
1	Surv	0.59	-14.8	1	Surv	0.57	-27.6
1	Biom	0.67	-21.5	1	Biom	0.64	-32.9
<u>1</u>	<u>Biom + Arr</u>	<u>0.76</u>	<u>-32.0</u>	<u>1</u>	<u>Biom + Arr</u>	<u>0.67</u>	<u>-35.8</u>
1	Biom + Germ	0.68	-21.3	1	Biom + Germ	0.66	-32.9
1	Biom + Surv	0.67	-20.3	1	Biom + Surv	0.64	-31.9
1	Biom + Arr + Germ	0.77	-30.7	1	Biom + Arr + Germ	0.69	-35.1
1	Biom + Arr + Surv	0.76	-30.4	1	Biom + Arr + Surv	0.69	-34.7
<hr style="border-top: 1px dashed black;"/>							
2	Biom + Arr + WL	0.78	-32.7	2	Biom + Arr + WL	0.74	-42.1
2	Biom + Arr + Grain	0.78	-33.5	2	Biom + Arr + Grain	0.75	-45.1
2	Biom + Arr + OM	0.78	-38.9	2	Biom + Arr + OM	0.68	-38.0
2	Biom + Arr + P	0.75	-30.0	2	Biom + Arr + P	0.68	-34.0
2	Biom + Arr + N	0.80	-34.7	2	Biom + Arr + N	0.73	-39.0
2	Biom + Arr + OM + WL	0.79	-39.1	2	Biom + Arr + Grain + WL	0.81	-51.9
2	Biom + Arr + OM + Grain	0.78	-37.1	2	Biom + Arr + Grain + OM	0.75	-43.8
<u>2</u>	<u>Biom + Arr + OM + P</u>	<u>0.77</u>	<u>-37.7</u>	2	Biom + Arr + Grain + P	0.74	-43.1
2	Biom + Arr + OM + N	0.82	-40.5	2	Biom + Arr + Grain + N	0.77	-45.4
2	Biom + Arr + OM + N + WL	0.85	-45.0	<u>2</u>	<u>Biom + Arr + Grain + WL + OM</u>	0.80	-50.6
2	Biom + Arr + OM + N + Grain	0.81	-38.5	2	Biom + Arr + Grain + WL + P	0.85	-56.1
<u>2</u>	<u>Biom + Arr + OM + N + P</u>	<u>0.81</u>	<u>-45.2</u>	<u>2</u>	<u>Biom + Arr + Grain + WL + N</u>	<u>0.87</u>	<u>-61.8</u>
2	Biom + Arr + OM + N + P + WL	0.81	-43.8	2	Biom + Arr + Grain + WL + N + OM	0.88	-63.2
2	Biom + Arr + OM + N + P + Grain	0.84	-44.9	2	Biom + Arr + Grain + WL + N + P	0.88	-61.0

Tiered forward selections on Shannon diversity of the vegetation

Table A4.4.3. Tiered forward selections of fixed effects in LMMs explaining Shannon diversity of the vegetation 1 and 2 years after restoration with the variance explained (R^2) and model fits (AIC) for each model. The effects of seed arrival (Arr), germination (Germ), seedling survival (Surv), and seedling growth (Biom) were tested in tier 1. In tier 2 (below the dashed line), additional effects of the abiotic variables water level (WL), soil organic matter content (OM), soil grain size (Grain), and soil extractable P (P), and N (N) were tested on the best model of tier 1. The best model in each tier (with >2 units AIC decrease for addition of a variable) was underlined. Transects were included as a random effect (intercept) in all models.

1 year after restoration				2 years after restoration			
#	Fixed effects	R^2	AIC	#	Fixed effects	R^2	AIC
1	None	0.00	79.9	1	None	0.00	25.4
1	Arr	0.00	81.9	1	Arr	0.00	27.4
1	Germ	0.17	77.1	1	Germ	0.24	19.8
<u>1</u>	<u>Surv</u>	0.61	51.8	<u>1</u>	<u>Surv</u>	<u>0.24</u>	<u>18.5</u>
1	Biom	0.11	78.5	1	Biom	0.06	25.7
1	Surv + Arr	0.59	53.7	1	Surv + Arr	0.23	20.5
1	Surv + Germ	0.60	53.5	1	Surv + Germ	0.30	17.9
<u>1</u>	<u>Surv + Biom</u>	<u>0.66</u>	<u>45.9</u>	1	Surv + Biom	0.24	20
1	Surv + Biom + Arr	0.65	47.8	2	Surv + WL	0.25	19.5
1	Surv + Biom + Germ	0.66	47.6	2	Surv + Grain	0.29	17.6
2	Surv + Biom + WL	0.67	46.9	2	Surv + OM	0.31	16.9
2	Surv + Biom + Grain	0.66	47.4	2	Surv + P avail	0.23	20.5
2	Surv + Biom + OM	0.67	47.0	2	Surv + N avail	0.25	19.3
2	Surv + Biom + P avail	0.66	47.5				
2	Surv + Biom + N avail	0.66	47.8				

Tiered forward selections on species number of the vegetation

Table A4.4.4. Tiered forward selections of fixed effects in Poisson GLMMs explaining species number of the vegetation 1 and 2 years after restoration with the variance explained (R^2) and model fits (AIC) for each model. The effects of seed arrival (Arr), germination (Germ), seedling survival (Surv), and seedling growth (Biom) were tested in tier 1. In tier 2 (below the dashed line), additional effects of the abiotic variables water level (WL), soil organic matter content (OM), soil grain size (Grain), and soil extractable P (P), and N (N) were tested on the best model of tier 1. The best model in each tier (with >2 units AIC decrease for addition of a variable) was underlined. Transects were included as a random effect (intercept) in all models.

1 year after restoration				2 years after restoration			
Tier	Fixed effects	R^2	AIC	Tier	Fixed effects	R^2	AIC
1	None	0.00	176.2	1	none	0.00	160.4
1	Arr	0.36	163.7	1	Arr	0.24	154.1
1	Germ	0.44	163.1	1	Germ	0.24	155.3
1	Surv	0.56	156.9	1	Surv	0.30	153.2
<u>1</u>	<u>Surv + Arr</u>	<u>0.59</u>	<u>150.8</u>	<u>1</u>	<u>Surv + Arr</u>	<u>0.37</u>	<u>149.9</u>
1	Surv + Germ	0.60	156.7	1	Surv + Germ	0.33	154.2
1	Surv + Arr + Germ	0.63	149.3	1	Surv + Arr + Germ	0.39	150.9
<u>2</u>	<u>Surv + Arr + WL</u>	<u>0.64</u>	<u>146.7</u>	2	Surv + Arr + WL	0.39	151.0
2	Surv + Arr + grain	0.61	151.9	2	Surv + Arr + grain	0.41	149.7
2	Surv + Arr + OM	0.62	151.4	2	Surv + Arr + OM	0.39	150.2
2	Surv + Arr + P avail	0.64	147.3	2	Surv + Arr + P avail	0.39	151.3
2	Surv + Arr + N avail	0.63	150.1	2	Surv + Arr + N avail	0.38	151.8
2	Surv + Arr + WL + grain	0.64	148.7				
2	Surv + Arr + WL + OM	0.64	148.6				
2	Surv + Arr + WL + P avail	0.64	148.1				
2	Surv + Arr + WL + N avail	0.65	148.4				

Appendix A4.5. Patterns in weighted Ellenberg F-values and Shannon diversity of the vegetation along the hydrological gradient 2 years after restoration

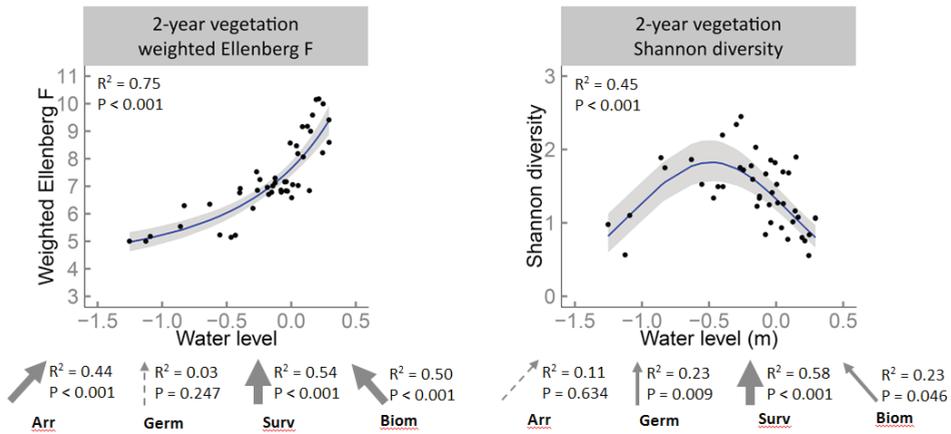


Figure A4.5.1. Patterns in abundance-weighted Ellenberg F-values and Shannon diversity of the vegetation along the hydrological gradient 2 years after restoration, as shaped by the processes of seed arrival (Arr), germination (Germ), seedling survival (Surv) and seedling growth (Biom). Negative water level values indicate water levels below the soil surface and positive values indicate water levels above the soil surface (flooding). Blue lines represent best model fits of LMMs to the field data (dots), with exponential relationships for weighted Ellenberg F-values and quadratic relationships for Shannon diversity. 95% confidence intervals (based on fixed effects only) are indicated by the grey ribbon, with model statistics in the upper or lower left corner, using transects as random effects (intercept) in all models. Linear relations between the processes and the vegetation were tested using LMMs with transects as random effect (intercept); model statistics are shown next to the grey arrows (thickness of the arrows proportionally to the R^2 value of the relation).

Appendix A4.6. Vegetation pattern of later successional stream riparian vegetation near the study locations

The vegetation patterns that were formed at the restored stream riparian zones 1 and 2 years after restoration closely resembled vegetation patterns of established (not recently restored) vegetations that occurred in the area closely to the research locations (52°13'1.84" N, 6°42'31.70" E; 51°42'44.50" N, 5°42'1.40" E; and 51°35'17.00" N, 5°16'59.20", near the Hagmolenbeek, Hooge Raam and Kleine Aa site respectively). Using a comparable monitoring design in the summer of 2013 (three transects per stream perpendicular to the channel, with five plots along the hydrological gradient per transect, and water levels measured from April/May up to August 2013), the vegetation communities showed an exponential increase in weighted Ellenberg F-value from the dry to the wet end of the gradients. This is highly comparable to the vegetation gradients we observed at the restored stream riparian zones 1 and 2 years after restoration (Fig. A4.6.1).

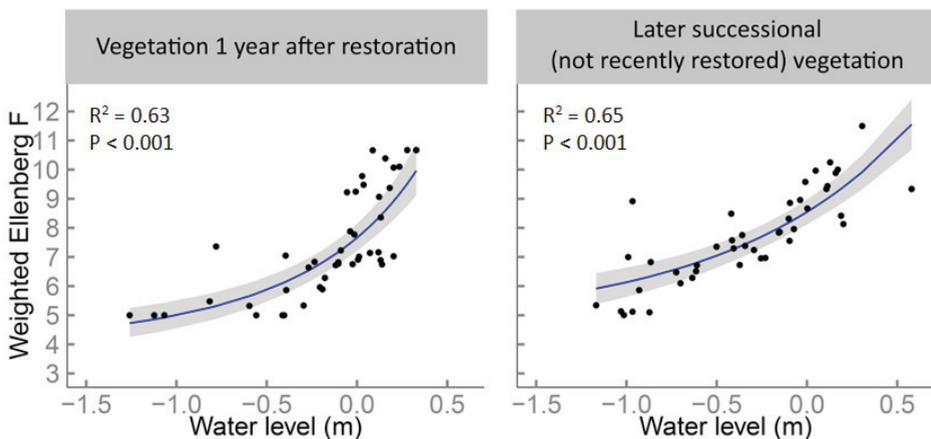


Figure A4.6.1. Pattern in weighted Ellenberg F-value along the hydrological gradient of the restored riparian zones 1 year after restoration (left panel) and of not recently restored vegetation communities near to the three research locations (right panel). Negative water level values indicate water levels below the soil surface and positive values indicate water levels above the soil surface (flooding). Blue lines represent best model fits of LMMs to the field data (dots), with exponential relationships for weighted Ellenberg F-values. 95% confidence intervals (based on fixed effects only) are indicated by the grey ribbon, with model statistics in the upper left corner, using transects as random effects (intercept) in all models.



Chapter 5

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

Rob G.A. Fraaije, Claire Poupin, Jos T.A. Verhoeven and Merel B.
Soons

ABSTRACT

Streams and their 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 worldwide, and although restoration projects have increased in the past decades, ecological improvement is lagging behind.

We assessed vegetation development in lowland stream valleys in the Netherlands in which innovative restoration measures to the stream and stream valleys were combined. This 'stream valley restoration' entailed the 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 (channelized) reaches.

The reduced channel dimensions led to higher flow velocities, which, through interaction with meandering, triggered a higher variability in flow and depth and the formation of sand banks at the land-water interface. Combined with enlargement of the floodplain, this promoted flooding in stream valleys and created wider environmental gradients. Vegetation clearly responded to these conditions. Plant diversity most strongly increased in the area covering the floodplain, the land-water interface and the shallow water habitat at the channel margins. Moreover, 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. Stream valley widening additionally increased beta diversity by opening up hydrological niches, strongly stimulating wetland species in areas with water tables between 0.0 and -0.3 m, but upland species as well.

Although many of the colonizing species were ruderals with high dispersal abilities, and more permanent vegetation responses are yet to be evaluated, our results demonstrated that the combined restoration measures were very effective in restoring habitat heterogeneity, leading to distinct short-term increases in diversity of many typical stream and riparian plant species. Overall, this stresses the importance of applying several restoration measures at once, considering the stream and its valley as a whole.

INTRODUCTION

Streams and their riparian zones are among the most diverse freshwater ecosystems on earth (Naiman & Décamps 1997). This diversity is generated by a high habitat heterogeneity, segregating species along axes of water flow, water depth and substrate

type in the aquatic zone (Haslam 1978; Madsen *et al.* 2001; Riis *et al.* 2001) and along the hydrological gradient in the riparian zone (Naiman & Décamps 1997; Pollock *et al.* 1998; Silvertown *et al.* 1999; Chapter 3, 4). Apart from niche segregation, differential arrival of plant species to specific (micro-)sites along the hydrological gradient also promotes plant diversity (M.B. Soons *et al.*, unpublished data; Chapter 4). In natural streams and riparian zones, intermediate disturbance levels (*cf.* Connell 1978) of water flow and flooding further promote plant diversity by limiting local competitive exclusion through uprooting, burial, or oxygen deprivation of established individuals, which generates space for immigrant individuals that arrive in large numbers via hydrochory (Nilsson *et al.* 2010). Unfortunately, these species coexistence mechanisms have been disrupted along streams across the world by human interventions like channelization, bank fixation, damming and water table regulation (Malmqvist & Rundle 2002). For lowland streams this has resulted in much wider and deeper stream channels with decreased flow velocities, which has reduced in-stream heterogeneity and the presence of lotic (running water) biota (Brooker 1985; Baattrup-Pedersen *et al.* 2005). Another consequence is the loss of riparian zones and concomitant moisture gradients, limiting both the extent and the heterogeneity of the riparian zone and reducing all species that depend on these niches (Baattrup-Pedersen *et al.* 2005).

Awareness of the declining biodiversity and ecosystem functions has triggered stream restoration in the past decades (Jähnig *et al.* 2011), which often encompassed restoration of hydrogeomorphic features. However, ecological improvement lagged behind in many of these restoration projects. Landscape-scale issues, like pollution and lack of nearby source populations, may severely hamper ecological success at the short term (Baattrup-Pedersen *et al.* 2000; Rohde *et al.* 2005; Palmer *et al.* 2010; Jähnig *et al.* 2010; Sarneel *et al.* 2011; Brederveld *et al.* 2011) and long time periods are required for ecological recovery and species accumulation (Helfield *et al.* 2012; Hasselquist *et al.* 2015). Despite these issues, restoration success was also often limited because habitat heterogeneity was not sufficiently restored (Januschke *et al.* 2014), or because measures focused only on specific aspects of the ecosystem while deteriorating other aspects, e.g. restoring a floodplain without paying attention to stream flow velocities (Verdonschot & Nijboer 2002). Therefore, more innovative restoration projects have been carried out in lowland streams recently, targeting the entire stream valley by combining a reduction of the channel dimension (channel narrowing and bed raising) to increase stream flow velocities and overbank flow, remeandering to increase habitat heterogeneity, and excavation of banks to restore a wide, v-shaped stream valley with gradually sloping riparian zones. Compared to conventional restoration, this 'stream valley restoration' rehabilitated a more natural range of stream flow velocities, flooding disturbances and environmental gradients. Now, we need to evaluate the ecological success of these improved measures, particularly for vegetation which

provides ecosystem functions including structure and habitat for other biota.

The studies reporting on similar stream restoration measures mostly indicate an increase in plant diversity. For the in-stream vegetation this increase was attributed to more diverse patterns of flow and depth (Langrehr *et al.* 2007; Lüderitz *et al.* 2011; Lorenz *et al.* 2012; Haase *et al.* 2013; Lorenz & Feld 2013), and, particularly for slower flowing systems like lowland streams, to increases in shallow areas (Biggs *et al.* 2001; Pedersen *et al.* 2006, 2007; Baart *et al.* 2010; Lorenz *et al.* 2012). For the riparian vegetation, increases were often attributed to increased flooding, induced by in-stream measures like bed raising, levee removal or placement of boulders (Biggs *et al.* 1998; Baatrup-Pedersen *et al.* 2000; Clarke & Wharton 2000; Helfield *et al.* 2007), or to the larger area for flow dynamics creating new mud, sand or gravel banks that are open for colonization by emergent pioneers (Biggs *et al.* 1998; Rohde *et al.* 2005; Pedersen *et al.* 2006; Jähnig *et al.* 2009; Januschke *et al.* 2011, 2014; Lorenz *et al.* 2012; Hering *et al.* 2015).

Information on increasing flow velocities in lower energy systems, potentially leading to more typically rheophilic plant species, and on widening of riparian zones, which may open up niches that had almost disappeared under channelized conditions, is however extremely rare. Pedersen *et al.* (2006) reported a strong relation between flow velocity variation and macrophyte assemblages in restored lowland streams, and Meyer *et al.* (2013) observed a shift to more rheophilic plant species in reconnected river side-channels. Wider riparian zones have been shown to lead to a higher diversity than unrestored riparian zones (Clarke & Wharton 2000), but introduction of propagules of wetland species, and creation of pools in the wider riparian zones contributed to the difference. Hering *et al.* (2015) investigated responses of wider riparian zones but particularly noted a rapid colonization of floodplain vegetation at the increased area at the land-water interface, while more niches may be opened along the riparian gradients. There is currently still a lack of information regarding restoration of hydrogeomorphic drivers of diversity, specifically on the effect of increased flow velocity in lowland streams and on widening of riparian zones. Studying these patterns is relevant for designing channel dimensions and riparian slopes in future restoration, and aids to understanding of vegetation trajectories following restoration.

Here, we quantify the responses of both the in-stream and the riparian vegetation to innovative stream valley restoration measures. We did this for five lowland streams by surveying hydrogeomorphology and vegetation along the complete range from the channel to the upbank. Specifically, we evaluated which species can be expected in the first years after restoration, focusing on life-history traits, dispersal traits, and habitat preferences in relation to the changes in hydrogeomorphology. Secondly, we evaluated how this translates into effects on plant diversity. We hypothesized that the higher in-stream flow velocities and increased spatial heterogeneity of in-stream flow velocities

would promote more rheophilic 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 species associated with wet to moist soils, thereby enhancing both total and beta diversity of riparian zones.

METHODS

We compared aquatic and riparian habitats of innovatively restored reaches with nearby unrestored reaches of lowland streams in the Netherlands. Habitat heterogeneity was assessed by measuring several physicochemical variables along stream valley transversal profiles (cross-sections). Responses of aquatic and riparian vegetation in plots along these cross-sections were analysed by comparing diversity metrics, and by comparing responses of plant species grouped per growth form (for in-stream vegetation) and Ellenberg F (moisture) classes (for riparian vegetation) between restored and unrestored reaches, paying specific attention to relations with hydrogeomorphic variables.

Study system

Streams and their riparian zones are characterized by a high spatiotemporal heterogeneity, sharp environmental gradients, and natural (flooding) disturbance regimes (Naiman *et al.* 1993; Naiman & Décamps 1997). They are also characterised by a naturally high connectivity, particularly through transport of organisms by water flow and flooding (hydrochory) (Wubs *et al.* 2016). These factors in combination support a high biodiversity. Lowland streams differ from other stream types by their more gentle slope (0-5‰) and low flow velocities (0.05-0.6 m s⁻¹), and typically show a close connection between precipitation, discharge and flooding of riparian zones (Verdonschot & Nijboer 2002). In the Netherlands, lowland streams mainly occur on sandy soils (Aeolian sand deposits) draining into the Rhine-Meuse delta (De Vries 1976). Almost all streams in the Netherlands have been channelized in the last century, as in many other regions of the world (Petts 1988; Poff *et al.* 1997; Malmqvist & Rundle 2002; Baattrup-Pedersen *et al.* 2005; Nilsson *et al.* 2005). In the past decades, increased awareness of habitat and biodiversity losses have prompted restoration projects targeting a more natural hydrology and morphology for streams and riparian zones (Verdonschot & Nijboer 2002; Jähnig *et al.* 2010; Brederveld *et al.* 2011)

We studied five lowland streams in the Netherlands of which reaches of 0.8-2 km stream length were restored between 2009 and 2011. The selected streams included the Hagemolenbeek (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 the Tungelroyse beek (TR; 51°14'42.7"

N, 5°53'12.7" E). The restoration involved innovative measures that affected the entire stream valley: reduction of the channel dimension (channel narrowing and bed raising) to increase stream flow velocities and overbank flow, re-meandering to increase habitat heterogeneity (not at HR), and excavation of banks to restore a widened, v-shaped stream valley with gradually sloping riparian zones at all streams. Compared to conventional restoration, this 'stream valley restoration' restored a more natural and varied range of stream flow velocities, flooding disturbances and environmental gradients. At each study location we selected a restored reach and an unrestored reach as nearby as possible (distances between 0.3 and 1.2 km) from the restored reaches. All pre-existing vegetation had been removed upon excavation. At HM only, the newly created riparian zone was sown with seeds of *Lolium perenne*, *Trifolium repens*, and *Phleum pratense* subsp. *pratense* (all species nomenclature following van der Meijden 2005) to diminish erosion immediately after restoration. Details on the research locations are available in Appendix A5.1.

Physicochemical variables

We mapped the stream and riparian zone transversal profiles using a GNSS-GPS RTK rover (Ashtech ProMark 800). To quantify hydrological conditions, water tables and surface water levels were continuously monitored 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. All measurements were performed on an hourly basis, with average values of the summer period (April–October) used for further water level analyses. Nutrient availability (extractable N and P) was measured on three combined soil cores (4 cm diameter, 10 cm depth) per riparian plot, and per in-stream section in April/May 2012 or 2013. Extractable P was determined using 0.5 M NaHCO₃ at pH of 8.5 (Olsen *et al.* 1954), followed by a colorimetric measurement using molybdate-ascorbic acid (Murphy & Riley 1962). Extractable ammonium and nitrate were determined with 0.4 M KCl extraction (Houba *et al.* 1995), followed by a colorimetric measurement on a continuous flow analyser (Skalar SA-40). Water quality parameters and discharge were obtained from measurement points near the study locations measured by local water boards, using average values of hourly discharge measurements in 2012 and averages of four water quality measurements in 2012/2013. Flow velocity was determined at three to four plots per in-stream transect, evenly spaced over the stream channel but at least 1/5 of the stream width remote from the bank, in May 2013. In-stream substrate type was recorded per in-stream plot by visual estimation of the dominant substrate in the first 10 cm of soil, separating stone (>60 mm diameter), gravel (3–60 mm), sand (0.25–3 mm), silt (<0.25 mm), clay or peat.

Vegetation surveys

To investigate the riparian vegetation along the entire hydrological gradient, three replicate transects of five plots (25 x 50 cm) were laid out across the riparian zone perpendicular to the stream channel within each reach (Fig. 5.1). In-stream vegetation was investigated by selecting three in-stream sections at the unrestored reach, and six in-stream sections at the restored reach. The larger number of sections at restored reaches was chosen because of the higher habitat heterogeneity, and in order to do this we selected three sections in straight stretches and three in bend stretches of each restored reach. Within each in-stream section five transects were investigated perpendicular to the stream flow, consisting of a continuous string of plots (25x25 cm) completely crossing the channel. Longitudinal distances between in-stream transects were always at least 5 meters. In each plot we registered species percent cover 2 years after restoration. In-stream vegetation surveys were carried out in June using a viewing tube. Riparian vegetation surveys were carried out in July or August. Due to time-constraints in-stream vegetation was only surveyed at the sites HM, KA and LB.

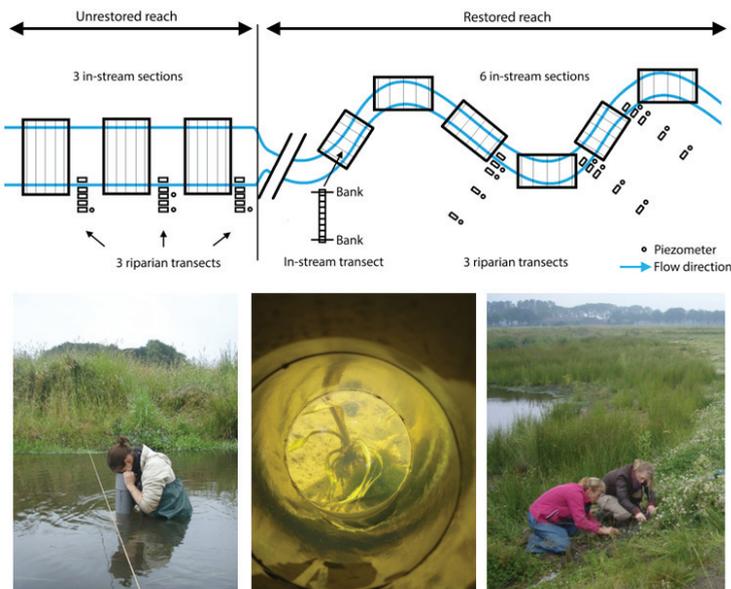


Figure 5.1. Overview of the experimental set-up in the field. At each study location, nine in-stream sections were selected, of which three in the unrestored reach, and six in the restored reach (three in straight stretches, and three in bend stretches). In each in-stream section five cross-channel transects were laid out perpendicularly to the stream flow, consisting of a continuous string of 25 x 25 cm plots, in which vegetation was surveyed using a viewing tube. 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 (see Chapter 3, 4 for more details). Piezometers were installed to monitor surface water or phreatic water levels at each riparian plot.

Plant and seed traits

We collected the following plant and seed traits: plant C-S-R functional signature (data from Hunt *et al.* 2004), functional groups regarding moisture preference as indicated by Ellenberg F-value (data from Ellenberg 1988, adjusted by Hill *et al.* 1999; grouping species to dry soil species (Ellenberg F <6), wetland species (Ellenberg F 7-10), and aquatic species (Ellenberg F >10)), and the dispersal traits plant life span (annual/perennial), seed buoyancy (percentage of seeds still floating after 1 week in water), seed mass (g), and seed terminal velocity (m s^{-1}) (from the LEDA traitbase, Knevel *et al.* 2003; Kleyer *et al.* 2008). For the in-stream vegetation we also classified species according to the functional habitat classification by Harvey *et al.* (2008). They linked surface flow conditions of running waters to local channel morphology and to biologically distinct vegetative and minerogenic units, ordering the following six functional habitats from higher flow velocities (rougher environments) to lower flow velocities (tranquil environments): 1) bed rock substrate and mosses, 2) cobble substrate, 3) gravel substrate and trailing vegetation (TV), 4) macro-algae and submerged fine-leaved macrophytes (MSF), 5) sand substrate, broad-leaved submerged macrophytes (MSB) and emergent macrophytes (ME), and 6) silt substrate and floating-leaved macrophytes (MF). We used the vegetative units of vascular plants to group the plant species in our surveys into growth forms associated to 1) fast flow (TV), 2) intermediate fast flow (MSF), 3) intermediate slow flow (MSB and ME), and slow flow (MF). TV included species rooting in the bank but trailing over the water (like *Agrostis stolonifera*), MSF included submerged aquatic plants with leaves at least 4 times longer than wide (*Potamogeton pectinatus* or *Ranunculus ssp.*), MSB included submerged species with leaves less than 4 times longer than wide (*Callitriche spp.*) as well as submerged linear-leaved plants (*Sparganium emersum*), ME included emergent broad-leaved herbs (*Lycopus europaeus*) as well as emergent reeds (*Typha latifolia*), and MF included rooting floating-leaved species (*Nuphar lutea*, *Potamogeton natans*) as well as free-floating species (*Hydrocharis morsus-ranae* and *Lemna spp.*). A complete overview of all identified species and their trait values is available in Appendix A5.3.

Data analysis

To test if physicochemical or vegetation parameters differed between restored and unrestored reaches, we compared statistical models that included the factor restoration as explanatory variable (separating restored and unrestored reaches) to models without this factor, using likelihood ratio tests to determine significance (p-values < 0.05). We used (generalized) linear mixed models (G)LMMs (R package lme4; Bates *et al.* 2014) with stream as a random effect (intercept) for analyses on the reach and transect scales, and with transect as a random effect (intercept) for analyses on the plot scale. Although transects were nested within stream in the study design,

streams were not included as an additional random effect for analyses on the plot scale. Exploratory analysis revealed that transects captured most variability of the mixed design while obtaining comparable but more stable results.

LMMs were used for analyses on physicochemical variables, community-weighted trait means of the vegetation (incidence-weighted) and beta deviation (see below) of the vegetation along the riparian gradient (with log- or arcsine-transformation of response values to improve normality when necessary, based on the Shapiro-Wilcoxon test). GLMMs were used for analyses on species number (poisson error distribution), for chance on growth-form occurrence and bray-curtis dissimilarity of the vegetation (binomial error distribution, as explained for bray-curtis dissimilarity in Ferrier *et al.* (2007)).

To account for differences in responses to restoration along the water level axis we simultaneously tested the effects of restoration, water level, and their interaction for several of the response variables using the above described models. For this we used a forward selection approach, selecting models with differing explanatory variables on the basis of model fits determined by the Akaike's Information Criterion (AIC). In each forward selection step, a fixed effect (restoration, water level, or lastly their interaction) yielding the lowest AIC was selected, with at least 2 units decrease in AIC for addition of a fixed effect (Burnham & Anderson 2002).

To analyse beta diversity (species turnover) along the riparian 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 `vegdist` function in R package `vegan` (Oksanen *et al.* 2015). We then tested the effect of water level distance (large distance for plots that were far apart, and small distance for adjacent plots), the effect of restoration, and their interaction on bray-curtis dissimilarity as described above. To correct for the possible influence of differences in alpha diversity between restored and unrestored reaches on species turnover along the riparian gradient, we used a null-model approach according to Myers *et al.* (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 from these simulated communities were used to correct the observed dissimilarities. Means of the null-model dissimilarities (of 2000 iterations) were subtracted from the observed dissimilarities, and divided by the standard deviation of the null-model dissimilarities, yielding a standardized effect size (beta-deviation), making the effect of water level differences on species turnover along the riparian gradient better comparable between restored and unrestored reaches.

RESULTS

Physicochemical variables

There were very clear differences in the physical and chemical characteristics between the restored and unrestored reaches. In-stream, the restored reaches were characterized by more shallow and narrow transversal channel dimensions, showing a strong increase in the area of shallow water habitats (2.4 versus 1.0 m wide), a fourfold increase in flow velocities (0.16 versus 0.04 m s⁻¹) and higher flow and depth variability (both 1.4 times higher) than at unrestored reaches (Fig. 5.2; Appendix A5.1 for an overview of all physicochemical variables). Deep water habitats were strongly reduced compared to unrestored reaches, the area of depth ranges between 0.6 and 1.5 m decreased 3.7 times (from 1.8 to 0.5 m wide) (Fig. 5.2). The substrate was always dominated by sand except at one unrestored section. The number of plots with silt as the dominant substrate decreased at all restored reaches on average from 45% to 1% of the plots (not significant due to large variation), and sand substrate significantly increased in dominance (from 43% to 78%).

Riparian zones in restored reaches were significantly wider (11.4 versus 2.3 m) than in unrestored reaches (Fig. 5.2), with strong increases of moist riparian area just above the water level (water tables of 0.0 – -0.3 m; 4.6 versus 0.6 m wide) and of moist zones with slightly deeper water tables (water tables of -0.3 to -0.6 m; 4.6 versus 0.7 m wide) (Fig. 5.6). Surface water levels showed larger fluctuations at restored reaches than at unrestored reaches (although not significant for all streams combined; $p = 0.0852$), leading to an average of 75.2 days year⁻¹ of overbank flow at restored reaches compared to 0.8 day year⁻¹ at unrestored reaches ($p < 0.001$), determined for the year 2012. Due to topsoil removal, soil N and P availability in the riparian zone and in the stream sediment were significantly lower at restored reaches (3.0 versus 6.5 mg kg⁻¹ dry soil for N availability and 4.5 versus 9.0 mg kg⁻¹ dry soil for P availability).

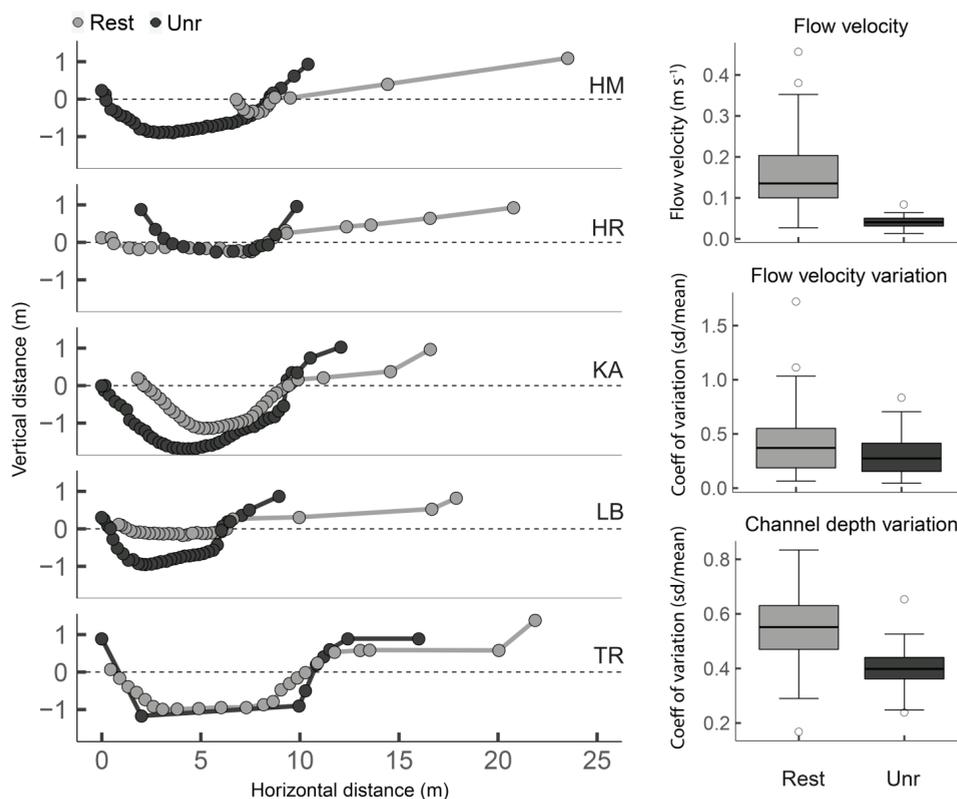


Figure 5.2. Transversal profiles of channels and riparian zones of restored (light grey) and unrestored (dark grey) reaches of the study locations Hagmolenbeek (HM), Hooge Raam (HR), Kleine Aa (KA), Luntersche beek (LB) and Tungalroyse beek (TR). The dashed horizontal line (at $y = 0$) represents the average surface water level in summer. Boxplots show the mean flow velocity, and in-stream transect-scale coefficients of variation for flow velocity and channel depth, with different greyscales for restored and unrestored reaches.

Plant life history and dispersal traits

In the first two years after restoration, the species colonizing the restored in-stream environment and riparian zones (see Appendix A5.2 for a complete list) were mainly pioneer species that disperse well. These species had significantly higher scores for the ‘ruderal’ strategy, lower scores for the ‘competitor’ strategy, and a shorter life span, lower seed mass, and higher seed dispersal ability by water (seed buoyancy) than at unrestored reaches (Fig. 5.3; Table 5.1). For the riparian vegetation, seed dispersal ability by wind (the inverse of terminal velocity) was also significantly higher at restored reaches.

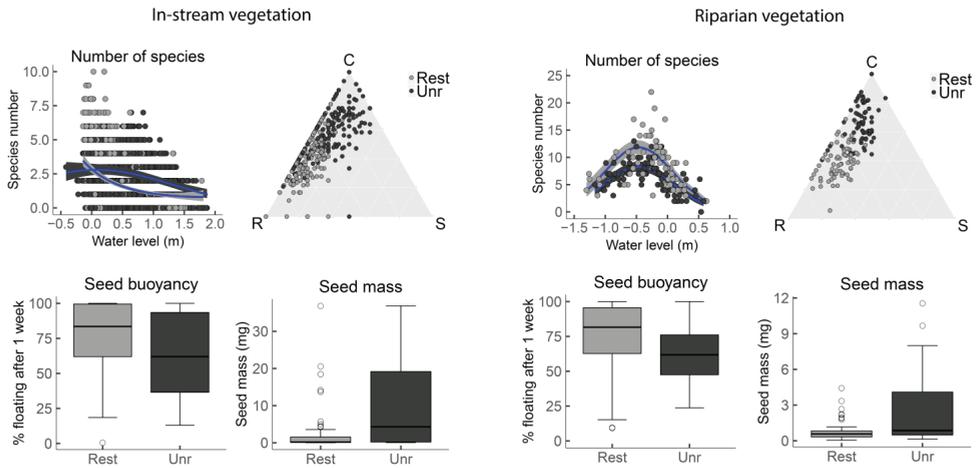


Figure 5.3. Overview of vegetation characteristics of in-stream vegetation (left four graphs) and riparian vegetation (right four graphs), showing plot-scale differences between restored and unrestored reaches (indicated by different greyscales) of the number of species along the water level gradient, functional signature in C-S-R space (the closer a point to a plant strategy, the higher its score for that strategy), and of the dispersal traits seed mass and seed buoyancy. Blue lines represent best model fits of GLMMs to the field data (dots), with the grey ribbons indicating 95% confidence intervals (based on fixed effects only).

Table 5.1. Means and standard deviations of in-stream and riparian vegetation characteristics for restored and unrestored reaches, showing species number on the reach, transect and plot scales, and plot-scale values for total plant cover, CSR functional signatures, life span (ordinal scale: annual (1), perennial (2)), seed buoyancy (% floating after 1 week), seed terminal velocity (m s^{-1}), seed mass (mg), and Ellenberg F-value. Significantly higher values (between restored and unrestored reaches) are bold and indicated with asterisks, corresponding to p-values of likelihood ratio tests listed below the table.

	In-stream				Riparian zone			
	Restored		Unrestored		Restored		Unrestored	
	Sd	Mean	Mean	Sd	Sd	Mean	Mean	Sd
Species richness								
Reach-scale	(1.7)	**40.0	27.0	(2.0)	(5.2)	***42.2	27.0	(5.7)
Transect-scale	(3.5)	10.7	10.7	(1.9)	(4.1)	***27.3	16.0	(4.7)
Plot-scale	(1.7)	2.1	2.4*	(1.4)	(4.2)	***8.6	6.3	(2.9)
Total plant cover	(36.3)	27	51.6***	(46.1)	(42.7)	82.8	114.7***	(45.8)
Life history:								
Competitors (C score)	(0.14)	0.45	0.56***	(0.17)	(0.11)	0.39	0.67***	(0.14)
Stress tolerators (S score)	(0.04)	0.01	0.06***	(0.08)	(0.07)	0.11	0.10	(0.08)
Ruderals (R score)	(0.14)	***0.54	0.38	(0.22)	(0.11)	***0.50	0.23	(0.12)
Life span	(0.29)	1.73	1.91***	(0.15)	(0.16)	1.76	1.97***	(0.08)
Dispersability:								
Seed buoyancy	(23.9)	*77.5	68.5	(23.9)	(24.5)	***76.1	62.0	(20.2)
Seed terminal velocity	(0.60)	1.44	2.23	(1.26)	(0.49)	1.70	2.31**	(0.59)
Seed mass	(2.16)	1.17	9.76***	(12.13)	(0.75)	0.74	2.37**	(2.86)
Habitat preference:								
Ellenberg F	(1.18)	10.57	10.9***	(0.68)	(1.75)	7.54	7.34	(1.55)

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

In-stream vegetation

In-stream vegetation showed a slow colonization after restoration, reaching only half of the coverage of unrestored reaches (27% versus 52%). Although the total number of in-stream species was higher at restored reaches than at unrestored reaches there was no difference on the transect scale, and a significantly lower diversity at the plot scale (Table 5.1). This was caused by a lower species diversity at deeper places in

restored reaches, while a comparable or higher species diversity occurred at the shallow habitats close to the banks (Fig. 5.2). Lower Ellenberg F-values indicated an increase of wetland or terrestrial species occurring in the stream, probably related to the increase in emergent plant species at the shallow areas (see below).

The decrease in floating species and slight increase in trailing species indicated a shift to more typically lotic in-stream vegetation communities than at unrestored reaches. Floating vegetation (associated to slow flow) was much less prevalent in restored reaches, showing a lower occurrence and diversity. Trailing vegetation (associated to fast flow) showed a higher occurrence and diversity at restored reaches than at unrestored reaches, although the very low number of occurrences limited detection of significant differences. The submerged broadleaved and emergent vegetation (associated to intermediate slow flow) showed no significant difference between restored and unrestored reaches, but emergent plant species were more prevalent at deeper places in unrestored reaches than at restored reaches, and the diversity of emergent plant species was much higher at the land-water interface of restored reaches. The submerged fine-leaved growth form (associated to intermediate fast flow) showed no clear response to restoration. Number of occurrences of this growth form was very low, so that model predictions marginally exceeded zero (Fig. 5.4).

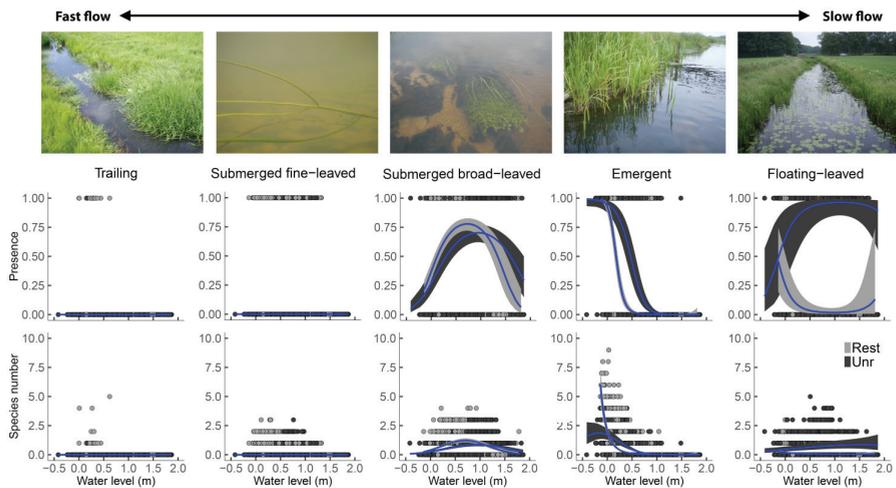


Figure 5.4. In-stream vegetation differences between restored and unrestored reaches (indicated by different greyscales), showing probability of occurrence (upper five graphs) and number of species (lower five graphs) of different growth forms per in-stream plot. Growth forms are ordered from left to right according to their association to more lotic, fast flowing habitats (left) or more lentic, slow flowing habitats (right), with the submerged broadleaved and emergent growth forms associated to the same flow conditions. Blue lines represent best model fits of GLMMs to the field data (dots). 95% confidence intervals (based on fixed effects only) are indicated by the grey ribbon.

Riparian vegetation

Riparian vegetation colonized quickly after restoration, reaching more than 80% coverage (compared to over 100% coverage at unrestored reaches; Table 5.1). Two years after restoration, species diversity of riparian vegetation was significantly higher at restored reaches than at unrestored reaches at the reach, transect as well as the plot scale, and at all elevations along the hydrological gradient (Fig. 5.2). Mean Ellenberg F-values of riparian vegetation did not differ significantly between restored and unrestored reaches and a quite similar vegetation zonation occurred along the riparian gradient 2 years after restoration, with species with high Ellenberg F-values close to the stream and those with lower values increasingly upslope (Fig. 5.6). However, the wider riparian zones of restored reaches resulted in a significantly higher species turnover with increasing elevation along the hydrological gradient (Fig. 5.5). This could be partly related to higher species diversities at restored reaches (independently of species occupying specific niches along the gradient). Still, however, species turnover as indicated by beta deviations (corrected for the higher overall species diversity at restored reaches) demonstrated a significantly higher species turnover at restored reaches. The largest increases in diversity occurred in the parts of the riparian zone that were most strongly enlarged, with water tables of 0.0 to -0.3 m (Fig. 5.6). Species associated to wet soils (Ellenberg F 7-9) strongly increased in diversity in this zone. Besides these species, however, also species more typical for dry soils (Ellenberg F4, F5) significantly increased in diversity in this zone. The area in the riparian zone with water tables between -0.3 and -0.6 m was also strongly enlarged, but diversity did not strongly increase at those places, only species with Ellenberg F 9 significantly increased there.

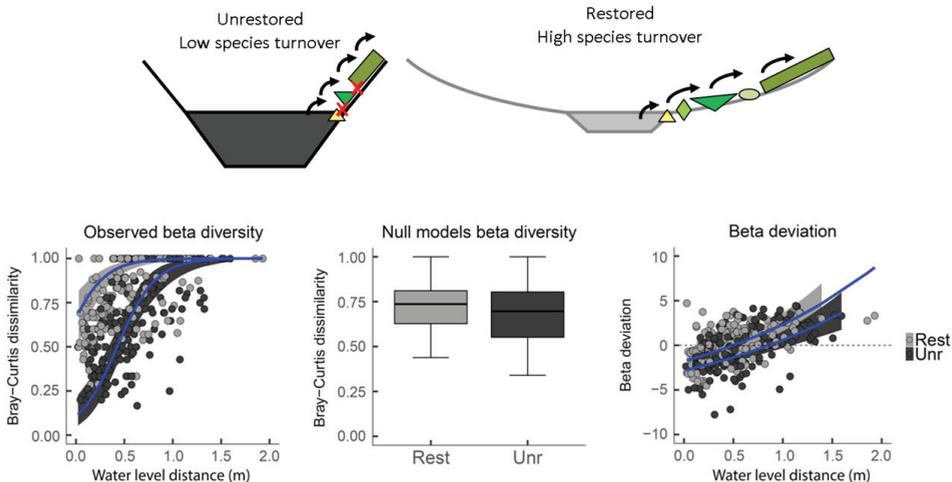


Figure 5.5. Spatial species turnover along the riparian hydrological gradients expressed by Bray-curtis dissimilarities between all pairwise combinations of plots in riparian transects, plotted against water level

distance between the plot pairs, with (a) the observed beta diversity, (b) beta diversity of null models; i.e. beta diversity generated by random distribution of species over the plots, keeping the number of species per plot constant (see Methods), and (c) standardized effect size of beta diversity (the observed beta diversity corrected for the null model outcomes), for the riparian zones of restored (light grey) and unrestored (dark grey) reaches. Blue lines represent best model fits of GLMMs to the field data (dots). 95% confidence intervals (based on fixed effects only) are indicated by the grey ribbon.

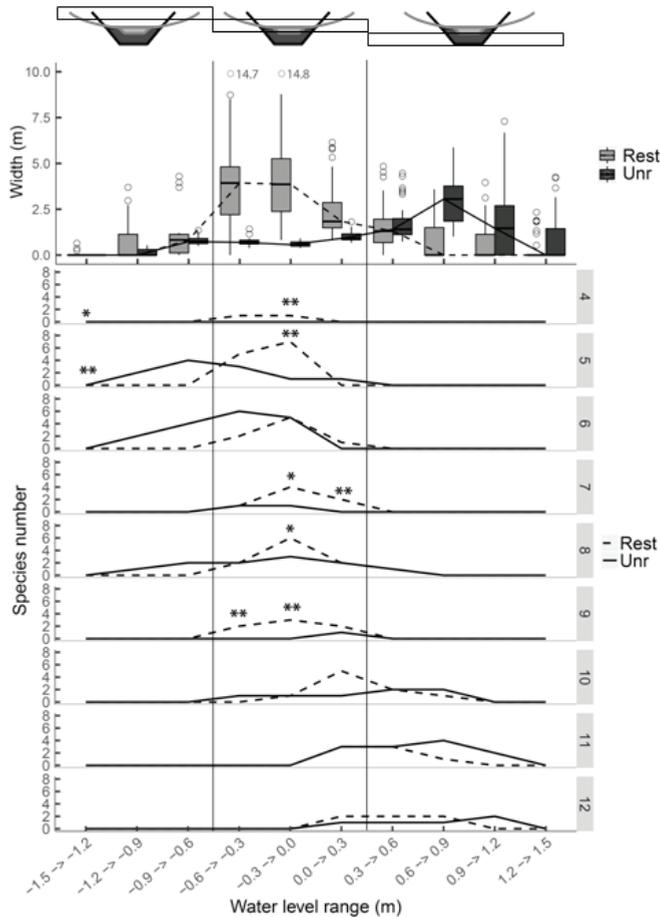


Figure 5.6. Boxplots showing the lateral widths (upper panel) of water level ranges in the stream channels (positive water level ranges) and in the riparian zones (negative water level ranges), with corresponding species numbers per Ellenberg F class (lower nine panels; Ellenberg F-values indicated on the right of the panels). Medians of boxplots of adjoining water level ranges are connected by continuous lines. Results are separated for restored reaches (light grey, and dashed lines) and unrestored reaches (dark grey, and solid lines). For species number per Ellenberg F class, only the lines connecting the medians are displayed. Asterisks indicate significantly higher species numbers at restored reaches for a water level range (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$).

DISCUSSION

Hydrogeomorphic changes by restoration

The reaches with restored hydrogeomorphology were characterized by significantly more shallow and narrow transversal channel dimensions, and much wider riparian zones with more gradual slopes. Reduction of the channel dimensions and enlargement of the floodplain stimulated flooding in the riparian zone, increasing flooding disturbance to the riparian vegetation and governing propagule arrival via hydrochory (Nilsson *et al.* 2010). Moreover, the reduced channel dimensions led to higher flow velocities, which interacted with meandering and vegetation patches, causing accelerated flow and erosion in outer bends and around vegetation, and reduced flow and sedimentation in inner bends and behind vegetation (Haslam 1978). These interactions invoked significantly higher spatial variability in flow and depths at the restored reaches, and stimulated the formation of bare sand banks at the land-water interface open for pioneer colonization (as also shown by Eekhout *et al.* (2015) for the same study locations). Besides the successfully restored flow velocities and dynamics of flow and floodings, the channel and riparian zone reconfiguration significantly widened habitat spaces from the shallow habitat at the channel margin (0.3 m water depth) up to the area with water tables of -0.6 m, on average from 2.3 m to 11.6 m wide. Excavation of new channels in sandy soils, and topsoil removal at riparian zones were probably the main cause of the strong reductions in silt substrate, and lower nutrient availabilities at the restored reaches. Higher flow velocities may however additionally have flushed silt substrates more strongly than at the unrestored reaches (Madsen *et al.* 2001).

Responses of plant species and diversity to hydrogeomorphic restoration

We hypothesized that the higher in-stream flow velocities and increased spatial heterogeneity of in-stream flow velocities would promote more rheophilic plant species and emergent macrophytes, and thereby total in-stream plant diversity. We further hypothesized that the wider and more spatially heterogeneous riparian zones would create more hydrological niches and thereby promote a range of species associated with wet to moist soils, thereby enhancing both total and beta diversity of riparian zones.

Plant diversity most strongly increased in the area covering the floodplain, the land-water interface and the shallow water habitat at the channel margins at all streams. This indicated that the increased flooding and flow-induced habitat heterogeneity led to a higher diversity of riparian plant species and a higher in-stream plant diversity at the channel margins. This is in line with previously reported responses to restored flooding regimes, where the combination of increased propagule

arrival and flooding disturbance to the vegetation, stimulated coexistence of pioneers and competitors, and therewith riparian zone diversity (Biggs *et al.* 1998; Baattrup-Pedersen *et al.* 2000; Clarke & Wharton 2000; Helfield *et al.* 2007). Moreover, this agrees with studies in which increased spatial dynamics induced by the stream flow stimulated the formation of bare sand, mud or gravel banks at the land-water interface, therewith promoting colonization of pioneer emergent species, enhancing overall diversity (Biggs *et al.* 1998; Rohde *et al.* 2005; Pedersen *et al.* 2006; Jähnig *et al.* 2009; Januschke *et al.* 2011, 2014; Lorenz *et al.* 2012; Hering *et al.* 2015). Widening of the shallow water habitats probably also enabled establishment of a larger number of species. Increases in shallow water habitat have previously been reported to lead to increased in-stream diversity (Biggs *et al.* 2001; Pedersen *et al.* 2006, 2007; Baart *et al.* 2010; Lorenz *et al.* 2012). Particularly emergent plant species benefitted from the increases in shallow water habitats, which was promoted by a process of colonization from the banks towards the channel (Henry & Amoros 1996), and stimulated by the more gradually sloping land-water interface at restored reaches (Pedersen *et al.* 2006).

Responses to the higher flow velocities were shown by a sharp decrease in floating species and increase of trailing species, indicating that, at the restored reaches, more typically lotic in-stream plant communities developed than at unrestored reaches (Harvey *et al.* 2008). Pedersen *et al.* (2006) also showed that restored streams were inhabited by in-stream plant communities more characteristic for natural undisturbed streams than for channelized streams. Meyer *et al.* (2013) reported clear shifts in macrophyte communities of river side channels in which flow velocity was increased after reconnection to the main river, leading to more rheophilic species. Flow velocities in these studies were however relatively high (around 0.4 m s^{-1} ; Meyer *et al.* 2013, or 0.24 m s^{-1} ; Pedersen *et al.* 2006). Our study indicates that mean flow velocities of 0.16 m s^{-1} were already effective in stimulating more rheophilic plant communities.

The higher flow velocities also promoted a slower in-stream vegetation colonization at the restored reaches, showing a lower cover and diversity in the central parts of the stream channels than at unrestored reaches. Flowing stream water can disturb developing seedlings by causing breakage or plant uprooting (Riis & Biggs 2003), and lead to limited propagule retention (Riis 2008). Previous studies found similar results 2 years after restoration, and attributed the slow colonization of in-stream vegetation mainly to the predominance of unconsolidated sandy substrates unsuitable for colonization, but also to limited upstream source populations (Biggs *et al.* 1998; Baattrup-Pedersen *et al.* 2000). Relatively close source populations were present upstream of our study sites (between 150 and 800 m) suggesting that dispersal limitation may not have played an overriding role in the slow colonization. It is rather likely that the combination of reduced propagule retention, and reduced establishment formed important mechanisms in the slow in-stream colonization.

At HM, vegetation in the channels developed faster than in the other stream sites (showing 41% mean cover versus 31% and 16% at KA and LB respectively). Probably the very narrow channels at HM allowed faster colonization from the banks towards the channels (Henry & Amoros 1996; Pedersen *et al.* 2006). However, longer periods of low flow velocities during the growing season at HM than at the other sites (personal observation), forming a window of opportunity for seedling establishment (Balke *et al.* 2014), may also have stimulated a more rapid in-stream vegetation development at this site.

Finally, widening of the riparian zones also clearly had an effect on the vegetation by significantly increasing species turnover (beta diversity) along the restored riparian gradients. The higher species turnover indicated that more hydrological niches (see Silvertown *et al.* 1999, 2015) could be utilized at the restored riparian zones, whereas these niches were too small at unrestored reaches to provide establishment and survival of species restricted to these niches. Previous studies investigating riparian zone widening also reported positive effects, but these effects mainly applied to the land-water interface (Hering *et al.* 2015), or were likely caused by the excavation of pools within the widened riparian zones (Clarke & Wharton 2000). To our knowledge, this is the first study where a higher beta diversity along restored stream riparian gradients was found to be related with the increased riparian area. In the widened riparian zones, we separately investigated functional groups (based on Ellenberg F-values) and discovered that wetland species (Ellenberg F7-10) clearly increased in diversity by restoration at the increased areas of moist soils. This is in line with the strong environmental filtering along hydrological gradients, which also explains the absence of aquatic species in these zones, which usually die quickly if their environment desiccates (Haslam 1978). Several dry-soil species (Ellenberg F 4-6), however, additionally benefitted from the widened area of wet soils in the riparian zone, which contrasts with their optimal habitat conditions.

Probably the lack of competition allowed these upland species to co-occur with wetland species, while they will be competitively displaced to the drier ends of the gradients when interspecific competition increases (Pickett & Bazzaz 1978; Wisheu & Keddy 1992; Silvertown *et al.* 1999). Increased interspecific competition may thus strongly affect subsequent vegetation development in later successional stages, which may also decrease the diversity among wetland species again (as comprehensively described for vegetation trajectories in newly created wetlands; Noon 1996). Disturbance dynamics by flooding may be of crucial importance to maintain the higher beta diversity by limiting expansion of competitors. Previous studies reported promising results, where increases in pioneer species after restoration were maintained when flow dynamics were strong enough to maintain rejuvenation (Rohde *et al.* 2005; Januschke *et al.* 2011). However, longer time-frames are necessary

to evaluate the effects of increased competition. In addition to flooding disturbances, the lower nutrient availability at restored reaches may be beneficial for maintaining the high beta diversity, as subordinate species may have a higher chance of utilizing their niche space (e.g. Wassen *et al.* 2005). Interactions between abiotic and biotic determinants of community structure are an interesting topic for future studies on stream restoration (e.g. see Kotowski *et al.* 2010).

Implications for future stream and stream valley restoration

The vegetation responses showed that increased flow and flooding dynamics, brought about by the reduction of channel dimensions and meandering, quickly increased diversity after restoration, and that higher stream flow velocities led to more typically lotic in-stream plant communities. Widening of riparian zones additionally stimulated biodiversity, by leading to a higher beta diversity, indicating that wide, gradually sloping stream valleys should be of key importance in future restoration projects. Particularly the combination of these measures was shown to be essential for successful restoration. Strong reduction of channel dimensions can only be applied when enough space is available in the stream valley for inundation during higher discharges, so that potentially harmful flow velocities in the channels and floodings at unwanted places, such as surrounding agricultural areas, can be avoided. Moreover, specifically the combination of higher flow velocities with meandering triggered a higher flow and depth variability which stimulated in-stream plant diversity. Prolonged periods of low flow velocities during the growing season are likely to stimulate the development of more lentic (stagnant or slow flowing water) species, and may lead to excess vegetation development which may cause flow obstruction. Such periods of low flow velocities are strongly influenced by catchment runoff regimes, emphasizing that catchment-scale factors are necessary for successful restoration. Overall, these results stress the importance of applying several restoration measures at once, focusing on the stream and its valley as a whole instead of carrying out restoration measures on only specific parts of the ecosystem.

Although colonization of riparian zones was faster than for the in-stream (channel) vegetation, both vegetation types showed a high proportion of ruderal species, and species with seed adaptations to wind dispersal (low terminal velocity; Soons *et al.* 2004), and water dispersal (high buoyancy; Nilsson *et al.* 2010), suggesting that many other species had difficulties in reaching the restored reaches. Dispersal limitation has earlier been shown to be a limiting factor for the success of stream restoration (Brederveld *et al.* 2011). This urges that landscape-level conservation and restoration planning should be carried out to optimize connectivity for target species (Verhoeven *et al.* 2008). Moreover, this indicates that introduction of target species, e.g. by hay transfer (Hölzel & Otte 2003; Klimkowska *et al.* 2007, 2010; Van Looy

2011), may form an additional key measure for successful restoration.

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Appendix A5.1 Details on the research locations and physicochemical parameters

We studied five lowland streams in the Netherlands of which reaches of 0.8-2 km stream length were restored. At each study location we selected a restored reach and an unrestored reach as nearby as possible (distances between 0.3 and 1.2 km) from the restored reaches. Restoration activities at the Hagmolenbeek (HM) were completed in June 2010, at the Hooge Raam (HR) in July 2009 (only the channel) and April 2011 (the riparian zone), at the Kleine Aa (KA) in July 2011, at the Luntersche Beek (LB) in November 2011, and at the Tengelroyse Beek (TR) in July 2011. Physicochemical variables clearly differed between restored and unrestored reaches (Table A5.1.1), which was very consistent among the different study locations (Table A5.1.2).

Table A5.1.1. Overview of physicochemical characteristics of restored and unrestored reaches. Values represent the means of measurements at all research locations, except for in-stream substrate, flow velocity (variation), channel depth (variation), and channel width, which were only assessed in detail for the study locations HM, LB and KA. The amount of fluctuation in surface water level (temporal coefficient of variation) and the duration of overbank flow apply to the year 2012. In-stream substrate types represent the percentage of plots in which the substrate was dominant. Significantly higher values (between restored and unrestored reaches) are bold and indicated with asterisks, corresponding to p-values of likelihood ratio tests listed below the table.

	Restored	Unrestored
Physical features		
Flow velocity (m s ⁻¹)	***0.16	0.04
Channel width (m)	5.32	8.22***
Channel depth (m)	0.42	0.78***
Riparian width (m)	***11.42	2.31
Spatial coeff var flow velocity (sd/mean)	*0.41	0.30
Spatial coeff var channel depth (sd/mean)	***0.55	0.40
Temp coeff var surf wl (sd/mean E-01)	0.17	0.14
Overbank flow (# days year ⁻¹)	***75.2	0.8
Nutrient availability (mg kg ⁻¹ dry soil)		
N avail stream sed	4.98	5.98***
P avail stream sed	5.72	8.54***
N avail riparian soil	2.27	6.49***
P avail riparian soil	4.78	10.90**
In-stream substrate (% of plots)		
Gravel	0.00	0.01
Clay	0.16	0.00
Peat	0.06	0.00
Sand	***0.78	0.43
Silt	0.01	0.45
Stones	0.00	0.11

*** p < 0.001, ** p < 0.01, *p < 0.05

Table A5.1.2. Overview of physicochemical characteristics of the study locations Hagsmolenbeek (HM), Hooge Raam (HR), Kleine Aa (KA), Luntersche beek (LB) and Tungelroyse beek (TR), for restored reaches (R) and unrestored reaches (U). In-stream substrate types represent the percentage of plots in which the substrate was dominant. The amount of fluctuation in surface water level (temporal coefficient of variation) and the duration of overbank flow apply to the year 2012.

	HM		HR		KA		LB		TR	
	R	U	R	U	R	U	R	U	R	U
Physical features										
Discharge (m ³ s ⁻¹)	0.12		0.15		0.85		0.40		1.09	
Flow velocity (m s ⁻¹)	0.16	0.03	-	-	0.15	0.05	0.17	0.04	-	-
Channel width (m)	2.8	8.7	8.3	5.0	7.7	9.3	5.5	6.7	9.8	-
Channel depth (m)	0.2	0.6	0.2	0.2	0.6	1.0	0.2	0.7	0.6	-
Riparian width (m)	15.3	2.2	15.0	2.2	11.9	2.6	10.5	2.5	14.1	2.0
Spatial coeff var flow velocity (sd/mean)	0.43	0.34	-	-	0.38	0.32	0.41	0.25	-	-
Spatial coeff var channel depth (sd/mean)	0.63	0.43	-	-	0.53	0.36	0.50	0.39	-	-
Temp coeff var surf wl (sd/mean E-01)	0.09	0.08	0.09	0.08	0.36	0.26	0.24	0.23	0.07	0.07
Overbank flow (# days year ⁻¹)	109	0	59	0	139	0	58	0	11	4
Nutrient availability										
N avail stream water (mg L ⁻¹)	-		5.46		3.45		2.71		4.38	
P avail stream water (mg L ⁻¹)	-		0.06		0.10		0.45		0.17	
N avail stream sedim (mg kg ⁻¹ dry soil)	6.95	7.33	0.38	0.60	3.55	7.04	4.44	3.56	3.73	14.34
P avail stream sedim (mg kg ⁻¹ dry soil)	3.85	6.93	0.77	1.11	6.36	8.69	6.95	10	3.23	8.42
N avail riparian soil (mg kg ⁻¹ dry soil)	2.80	6.69	0.54	5.42	5.47	6.41	1.16	6.90	1.39	7.03
P avail riparian soil (mg kg ⁻¹ dry soil)	9.59	5.00	0.50	5.12	6.53	9.11	3.85	26.04	3.43	9.22
In-stream substrate (% of plots)										
Gravel	0	0	-	-	0.01	0.04	0	0	-	-
Clay	0.46	0	-	-	0	0	0.01	0	-	-
Peat	0	0	-	-	0	0	0.16	0	-	-
Sand	0.54	0	-	-	0.99	0.77	0.81	0.52	-	-
Silt	0	1.00	-	-	0	0.18	0.02	0.16	-	-
Stones	0	0	-	-	0	0	0	0.32	-	-

Appendix A5.2 List of species in the vegetation

Table A5.2.1 List of species observed in the riparian plots (of which the lowest plots were in-stream) with the percentage of occurrence in the plots, separately for restored and unrestored reaches. Species are ordered from high to low occurrence.

RIPARIAN VEGETATION			
Restored		Unrestored	
Species	% of plots	Species	% of plots
<i>Agrostis stolonifera</i>	46.7	<i>Phalaris arundinacea</i>	64.0
<i>Juncus bufonius</i>	33.3	<i>Urtica dioica</i>	60.0
<i>Lolium perenne</i>	33.3	<i>Poa trivialis</i>	42.7
<i>Lycopus europaeus</i>	33.3	<i>Holcus lanatus</i>	33.3
<i>Juncus articulatus</i>	32.0	<i>Elytrigia repens</i>	29.3
<i>Trifolium repens</i>	30.7	<i>Holcus mollis</i>	26.7
<i>Epilobium ciliatum</i>	29.3	<i>Glyceria maxima</i>	25.3
<i>Callitriche sp*</i>	28.0	<i>Convolvulus sepium</i>	22.7
<i>Poa trivialis</i>	28.0	<i>Arrhenatherum elatius</i>	21.3
<i>Juncus effusus</i>	26.7	<i>Glechoma hederacea</i>	21.3
<i>Conyza canadensis</i>	22.7	<i>Phragmites australis</i>	16.0
<i>Ranunculus repens</i>	22.7	<i>Carex riparia</i>	14.7
<i>Phleum pratense ssp pratense</i>	21.3	<i>Alopecurus pratensis</i>	13.3
<i>Bidens frondosa</i>	20.0	<i>Lysimachia nummularia</i>	12.0
<i>Lemna minor</i>	16.0	<i>Aegopodium podagraria</i>	10.7
<i>Rorippa palustris</i>	16.0	<i>Dactylis glomerata</i>	10.7
<i>Holcus lanatus</i>	14.7	<i>Lemna minor</i>	9.3
<i>Myosotis scorpioides</i>	14.7	<i>Rumex obtusifolius</i>	9.3
<i>Phalaris arundinacea</i>	14.7	<i>Agrostis stolonifera</i>	8.0
<i>Gnaphalium uliginosum</i>	13.3	<i>Lolium perenne</i>	8.0
<i>Mentha aquatica</i>	13.3	<i>Lycopus europaeus</i>	8.0
<i>Poa annua</i>	13.3	<i>Festuca arundinacea</i>	8.0
<i>Taraxacum officinale</i>	13.3	<i>Cardamine sp*</i>	6.7
<i>Ranunculus sceleratus</i>	10.7	<i>Persicaria amphibia</i>	6.7
<i>Salix alba</i>	10.7	<i>Callitriche sp*</i>	5.3
<i>Alisma plantago-aquatica</i>	9.3	<i>Juncus effusus</i>	5.3
<i>Alnus glutinosa</i>	9.3	<i>Myosotis scorpioides</i>	5.3
<i>Cardamine sp*</i>	9.3	<i>Spirodela polyrhiza</i>	5.3
<i>Galium palustre</i>	9.3	<i>Agrostis capillaris</i>	5.3
<i>Salix caprea/cinerea/reichtardii</i>	9.3	<i>Calamagrostis canescens</i>	5.3
<i>Typha latifolia</i>	9.3	<i>Cardamine flexuosa</i>	5.3
<i>Bidens cernua</i>	8.0	<i>Equisetum arvense</i>	5.3
<i>Phragmites australis</i>	8.0	<i>Scirpus sylvaticus</i>	5.3
<i>Plantago major ssp major</i>	8.0	<i>Symphytum officinale</i>	5.3
<i>Potamogeton pusillus</i>	8.0	<i>Ranunculus repens</i>	4.0
<i>Sonchus arvensis</i>	8.0	<i>Sparganium erectum</i>	4.0
<i>Sparganium erectum</i>	8.0	<i>Elodea nuttallii</i>	4.0
<i>Crepis capillaris</i>	6.7	<i>Cirsium arvense</i>	4.0
<i>Epilobium hirsutum</i>	6.7	<i>Ceratophyllum demersum</i>	4.0
<i>Equisetum palustre</i>	6.7	<i>Galium aparine</i>	4.0
<i>Glyceria fluitans</i>	6.7	<i>Juncus acutiflorus</i>	4.0
<i>Lotus pedunculatus</i>	6.7	<i>Epilobium ciliatum</i>	2.7
<i>Unknown seedling 1</i>	6.7	<i>Phleum pratense ssp pratense</i>	2.7
<i>Ranunculus repens/sceleratus</i>	6.7	<i>Alnus glutinosa</i>	2.7
<i>Rumex obtusifolius</i>	6.7	<i>Stellaria media</i>	2.7

<i>Sparganium emersum</i>	6.7	<i>Festuca rubra</i>	2.7
<i>Stellaria media</i>	6.7	<i>Filipendula ulmaria</i>	2.7
<i>Cerastium glomeratum</i>	5.3	<i>Angelica sylvestris</i>	2.7
<i>Digitaria ischaemum</i>	5.3	<i>Anthriscus sylvestris</i>	2.7
<i>Elodea nuttallii</i>	5.3	<i>Potamogeton natans</i>	2.7
<i>Epilobium parviflorum</i>	5.3	<i>Vicia cracca</i>	2.7
<i>Juncus conglomeratus</i>	5.3	<i>Juncus articulatus</i>	1.3
<i>Lythrum salicaria</i>	5.3	<i>Bidens frondosa</i>	1.3
<i>Crepis capillaris/Taraxacum officinale</i>	4.0	<i>Potamogeton pusillus</i>	1.3
<i>Eupatorium cannabinum</i>	4.0	<i>Crepis capillaris</i>	1.3
<i>Festuca pratensis</i>	4.0	<i>Epilobium hirsutum</i>	1.3
<i>Myosotis laxa ssp cespitosa</i>	4.0	<i>Equisetum palustre</i>	1.3
<i>Persicaria lapathifolia</i>	4.0	<i>Sparganium emersum</i>	1.3
<i>Spirodela polyrhiza</i>	4.0	<i>Elodea canadensis</i>	1.3
<i>Urtica dioica</i>	4.0	<i>Achillea millefolium</i>	1.3
<i>Zannichellia palustris</i>	4.0	<i>Alisma plantago-aquatica/lanceolatum</i>	1.3
<i>Alopecurus geniculatus</i>	2.7	<i>Bidens tripartita</i>	1.3
<i>Betula pendula/pubescens</i>	2.7	<i>Cerastium sp*</i>	1.3
<i>Carex pseudocyperus</i>	2.7	<i>Hydrocharis morsus-ranae</i>	1.3
<i>Cerastium fontanum ssp vulgare</i>	2.7	<i>Nymphoides peltata</i>	1.3
<i>Chenopodium album</i>	2.7	<i>Plantago lanceolata</i>	1.3
<i>Cirsium arvense</i>	2.7	<i>Poa pratensis</i>	1.3
<i>Elodea canadensis</i>	2.7	<i>Rumex acetosa</i>	1.3
<i>Glyceria maxima</i>	2.7	<i>Scutellaria galericulata</i>	1.3
<i>Gnaphalium luteo-album</i>	2.7	<i>Unknown seedling 2</i>	1.3
<i>Lemna trisulca</i>	2.7	<i>Unknown seedling 3</i>	1.3
<i>Matricaria chamomilla</i>	2.7	<i>Unknown seedling 4</i>	1.3
<i>Persicaria maculosa</i>	2.7	<i>Unknown seedling 5</i>	1.3
<i>Rumex acetosella</i>	2.7	<i>Unknown seedling 6</i>	1.3
<i>Senecio vulgaris</i>	2.7	<i>Unknown seedling 7</i>	1.3
<i>Achillea ptarmica</i>	1.3		
<i>Arrhenatherum elatius</i>	1.3		
<i>Bidens frondosa/cernua/tripartita</i>	1.3		
<i>Eleocharis acicularis</i>	1.3		
<i>Epilobium montanum/tetragonum</i>	1.3		
<i>Equisetum fluviatile</i>	1.3		
<i>Festuca filiformis</i>	1.3		
<i>Festuca gigantea</i>	1.3		
<i>Festuca rubra</i>	1.3		
<i>Filipendula ulmaria</i>	1.3		
<i>Hypochaeris radicata</i>	1.3		
<i>Isolepis setacea</i>	1.3		
<i>Lysimachia vulgaris</i>	1.3		
<i>Unknown seedling 8</i>	1.3		
<i>Sagina procumbens</i>	1.3		
<i>Salix caprea</i>	1.3		
<i>Salix fragilis/alba x fragilis</i>	1.3		
<i>Salix viminalis</i>	1.3		
<i>Stellaria holostea</i>	1.3		
<i>Tanacetum vulgare</i>	1.3		
<i>Tripleurospermum maritimum</i>	1.3		
<i>Veronica catenata</i>	1.3		
<i>Vulpia bromoides</i>	1.3		

*Callitriche sp**: *Callitriche platycarpa/obtusangula/stagnalis*

*Cardamine sp**: *Cardamine amara/flexuosa/hirsuta/pratensis*

*Cerastium sp**: *Cerastium arvense/fontanum/glomeratum/semidecandrum*

Table A5.2.2 List of species observed in the in-stream plots with the percentage of occurrence in the plots, separately for restored and unrestored reaches. Species are ordered from high to low occurrence.**IN-STREAM VEGETATION**

Restored		Unrestored	
Species	% of plots	Species	% of plots
<i>Callitriche sp*</i>	43.6	<i>Lemna minor</i>	38.7
<i>Lemna minor</i>	29.0	<i>Nuphar lutea</i>	28.1
<i>Elodea nuttallii</i>	22.9	<i>Callitriche sp*</i>	24.4
<i>Sparganium emersum</i>	18.7	<i>Elodea nuttallii</i>	23.9
<i>Zannichellia palustris</i>	11.8	<i>Potamogeton natans</i>	18.8
<i>Potamogeton pusillus</i>	11.6	<i>Sparganium emersum</i>	17.8
<i>Glyceria maxima</i>	7.3	<i>Glyceria maxima</i>	12.6
<i>Phalaris arundinacea</i>	6.2	<i>Potamogeton pusillus</i>	12.3
<i>Agrostis stolonifera</i>	6.0	<i>Sagittaria sagittifolia</i>	9.1
<i>Myosotis scorpioides</i>	5.5	<i>Zannichellia palustris</i>	7.5
<i>Juncus articulatus</i>	4.4	<i>Sparganium erectum</i>	5.3
<i>Alopecurus geniculatus</i>	4.1	<i>Phalaris arundinacea</i>	5.0
<i>Glyceria fluitans</i>	3.2	<i>Spirodela polyrhiza</i>	4.6
<i>Spirodela polyrhiza</i>	3.1	<i>Phragmites australis</i>	4.6
<i>Juncus bufonius</i>	2.9	<i>Potamogeton alpinus</i>	4.3
<i>Phragmites australis</i>	2.1	<i>Ceratophyllum demersum</i>	3.5
<i>Ranunculus repens</i>	1.9	<i>Lemna trisulca</i>	3.3
<i>Alisma plantago-aquatica</i>	1.9	<i>Carex riparia</i>	2.3
<i>Mentha aquatica</i>	1.3	<i>Myosotis scorpioides</i>	1.8
<i>Typha latifolia</i>	1.2	<i>Equisetum fluviatile</i>	1.6
<i>Juncus effusus</i>	1.0	<i>Alisma plantago-aquatica</i>	1.3
<i>Rorippa palustris</i>	1.0	<i>Mentha aquatica</i>	1.0
<i>Nasturtium officinale</i>	0.9	<i>Hydrocharis morsus-ranae</i>	0.7
<i>Veronica anagallis-aquatica</i>	0.9	<i>Scirpus sylvaticus</i>	0.7
<i>Ceratophyllum demersum</i>	0.8	<i>Elytrigia repens</i>	0.6
<i>Epilobium ciliatum</i>	0.8	<i>Berula erecta</i>	0.4
<i>Lemna trisulca</i>	0.8	<i>Veronica anagallis-aquatica</i>	0.4
<i>Rorippa amphibia</i>	0.8	<i>Iris pseudacorus</i>	0.3
<i>Bidens frondosa</i>	0.7	<i>Carex rostrata</i>	0.3
<i>Eleocharis acicularis</i>	0.7	<i>Eleocharis palustris</i>	0.3
<i>Poa annua</i>	0.7	<i>Poa trivialis</i>	0.3
<i>Potamogeton crispus</i>	0.7	<i>Urtica dioica</i>	0.3
<i>Ranunculus sceleratus</i>	0.7	<i>Alopecurus pratensis</i>	0.2
<i>Potamogeton natans</i>	0.6	<i>Epilobium hirsutum</i>	0.2
<i>Catabrosa aquatica</i>	0.6	<i>Agrostis stolonifera</i>	0.1
<i>Nuphar lutea</i>	0.6	<i>Alisma lanceolatum</i>	0.1
<i>Persicaria amphibia</i>	0.6	<i>Catabrosa aquatica</i>	0.1
<i>Galium palustre</i>	0.5	<i>Lycopus europaeus</i>	0.1

<i>Lycopus europaeus</i>	0.5	<i>Ranunculus sceleratus</i>	0.1
<i>Myriophyllum spicatum</i>	0.5	<i>Rorippa amphibia</i>	0.1
<i>Sagittaria sagittifolia</i>	0.5	<i>Bidens frondosa</i>	0.1
<i>Elytrigia repens</i>	0.3	<i>Lysimachia nummularia</i>	0.1
<i>Lysimachia nummularia</i>	0.3	<i>Myriophyllum spicatum</i>	0.1
<i>Epilobium hirsutum</i>	0.3	<i>Oenanthe aquatica</i>	0.1
<i>Poa trivialis</i>	0.3	<i>Potamogeton crispus</i>	0.1
<i>Trifolium repens</i>	0.2	<i>Rumex acetosa</i>	0.1
<i>Potamogeton alpinus</i>	0.2	<i>Rumex hydrolapathum</i>	0.1
<i>Schoenoplectus lacustris</i>	0.2	<i>Scutellaria galericulata</i>	0.1
<i>Azolla filiculoides</i>	0.1	<i>Solanum dulcamara</i>	0.1
<i>Berula erecta</i>	0.1		
<i>Equisetum palustre</i>	0.1		
<i>Gnaphalium uliginosum</i>	0.1		
<i>Persicaria maculosa</i>	0.1		
<i>Scirpus sylvaticus</i>	0.1		
<i>Sparganium erectum</i>	0.1		
<i>Bidens tripartita</i>	0.1		
<i>Cirsium arvense</i>	0.1		
<i>Echinochloa crus-galli</i>	0.1		
<i>Eleocharis palustris</i>	0.1		
<i>Equisetum fluviatile</i>	0.1		
<i>Hydrocharis morsus-ranae</i>	0.1		
<i>Lythrum salicaria</i>	0.1		
<i>Oenanthe aquatica</i>	0.1		
<i>Phleum pratense ssp pratense</i>	0.1		
<i>Ranunculus peltatus</i>	0.1		

Callitriche sp*: *Callitriche platycarpa/obtusangula/stagnalis*

Table A5.2.3 Overview of species characteristics and traits of all species observed in the in-stream and/or riparian plots. In-stream growth forms are only given for species that were observed in the in-stream vegetation survey listing emergent (EM), floating (FL), submerged broad-leaved (SBL), submerged fine-leaved (SFL) and trailing (TR). Missing values are indicated with a hyphen.

species	CSR class	C score	S score	R score	Life span	Ellenberg F	Buoyancy (% floating after 1 week)	Seed mass (mg)	Terminal velocity (m s ⁻¹)	In-stream growth form
<i>Achillea millefolium</i>	CR/CSR	0.42	0.17	0.42	Per 4	-	0.14	1.45	-	
<i>Achillea ptarmica</i>	CR/CSR	0.42	0.17	0.42	Per 8	-	98.5	0.15	1.9	-
<i>Aegopodium podagraria</i>	CR/CSR	0.42	0.17	0.42	Per 5	-	2.73	3.7	-	
<i>Agrostis capillaris</i>	CSR	0.33	0.33	0.33	Per 5	-	81.5	0.06	1.17	-
<i>Agrostis stolonifera</i>	CR	0.5	0	0.5	Per 6	-	100	0.02	1.27	EM
<i>Alisma lanceolatum</i>	R/CR	0.25	0	0.75	Per 10	-	84.5	0.35	1.62	EM
<i>Alisma plantago-aquatica</i>	R/CR	0.25	0	0.75	Per 10	-	0.28	1.7	EM	
<i>Alisma plantago-aquatica/lanceolatum</i>	R/CR	0.25	0	0.75	Per 10	-	84.5	0.32	1.66	-
<i>Alnus glutinosa</i>	SC	0.5	0.5	0	Per 8	-	1.08	2.43	-	
<i>Alopecurus geniculatus</i>	CR	0.5	0	0.5	- 7	-	42.5	0.38	-	EM
<i>Alopecurus pratensis</i>	C/CSR	0.67	0.17	0.17	Per 5	-	13	0.45	2.18	EM
<i>Angelica sylvestris</i>	C/CR	0.75	0	0.25	Per 8	-	89	1.31	1.81	-
<i>Anthriscus sylvestris</i>	CR	0.5	0	0.5	Per 5	-	5.18	3.68	-	
<i>Arrhenatherum elatius</i>	C/CSR	0.67	0.17	0.17	Per 5	-	0	2.71	2.62	-
<i>Azolla filiculoides</i>	-	-	-	-	Per 11	-	-	-	-	FL
<i>Berula erecta</i>	CR	0.5	0	0.5	Per 10	-	0.5	-	-	EM
<i>Betula pendula/pubescens</i>	SC	0.5	0.5	0	Per 6	-	75.8	0.15	0.58	-
<i>Bidens cernua</i>	R/CR	0.25	0	0.75	Ann 9	-	98	1	1.5	-
<i>Bidens frondosa</i>	-	-	-	-	Ann -	-	99	2.74	1.81	EM
<i>Bidens frondosa/cernua/tripartita</i>	R/CR	0.25	0	0.75	Ann 8.5	-	98.5	2.11	1.8	-
<i>Bidens tripartita</i>	R/CR	0.25	0	0.75	Ann 8	-	2.59	2.09	EM	
<i>Calamagrostis canescens</i>	C/SC	0.75	0.25	0	Per 9	-	60	0.09	0.79	-
<i>Callitriche platycarpa/obtusangula/stagnalis</i>	CR_R/CR_R/CR	0.33	0	0.67	Ann 10.7	-	0.09	1.13	SBL	
<i>Cardamine sp*</i>	*	0.17	0.23	0.6	- 7.3	-	9.5	0.27	2.37	-
<i>Cardamine flexuosa</i>	R/SR	0	0.25	0.75	- 7	-	9.5	0.13	-	-
<i>Carex pseudocyperus</i>	C/CSR	0.67	0.17	0.17	- 9	-	0.78	2.67	-	
<i>Carex riparia</i>	C/SC	0.75	0.25	0	Per 8	-	99.5	1.69	3.13	EM
<i>Carex rostrata</i>	SC	0.5	0.5	0	Per 10	-	100	0.81	2.61	EM
<i>Catabrosa aquatica</i>	CR	0.5	0	0.5	Per 9	-	83.5	0.32	-	EM
<i>Cerastium sp*</i>	*	0.08	0.33	0.58	- 4.3	-	6.75	0.09	1.98	-
<i>Cerastium fontanum ssp vulgare</i>	R/CSR	0.17	0.17	0.67	Per 5	-	0.12	2.27	-	
<i>Cerastium glomeratum</i>	R/SR	0	0.25	0.75	Ann 5	-	6	0.05	1.88	-
<i>Ceratophyllum demersum</i>	CR	0.5	0	0.5	Per 12	-	-	-	-	FL
<i>Chenopodium album</i>	R/CR	0.25	0	0.75	Ann 5	-	0.67	-	-	
<i>Cirsium arvense</i>	C	1	0	0	Per 6	-	93.5	1.17	0.28	EM

Table A5.2.3 continued

species	CSR class	C score	S score	R score	Life span	Ellenberg F	Buoyancy (% floating after 1 week)	Seed mass (mg)	Terminal velocity (m s ⁻¹)	In-stream growth form
<i>Convolvulus sepium</i>	C/CR	0.75	0	0.25	Per 8		-	33.9	5.01	-
<i>Conyza canadensis</i>	R/CR	0.25	0	0.75	Ann 4		-	0.05	0.24	-
<i>Crepis capillaris</i>	R/SR	0	0.25	0.75	- 4		-	0.14	0.36	-
<i>Crepis capillaris/Taraxacum officinale</i>	R/SR_R/CSR	0.08	0.21	0.71	- 4.5		-	0.39	0.49	-
<i>Dactylis glomerata</i>	C/CSR	0.67	0.17	0.17	Per 5		-	0.78	2.82	-
<i>Digitaria ischaemum</i>	-	-	-	-	Ann 4		-	-	1.34	-
<i>Echinochloa crus-galli</i>	-	-	-	-	Ann -		-	-	3.17	EM
<i>Eleocharis acicularis</i>	R/SR	0	0.25	0.75	Per 10		100	-	3.52	SFL
<i>Eleocharis palustris</i>	SC/CSR	0.42	0.42	0.17	Per 10		-	0.96	-	EM
<i>Elodea canadensis</i>	CR	0.5	0	0.5	Per 12		-	-	-	-
<i>Elodea nuttallii</i>	CR	0.5	0	0.5	Per 12		-	-	-	SBL
<i>Elytrigia repens</i>	C/CR	0.75	0	0.25	Per 5		-	1.83	2.54	EM
<i>Epilobium ciliatum</i>	CSR	0.33	0.33	0.33	Per 6		94.5	0.06	0.2	EM
<i>Epilobium hirsutum</i>	C	1	0	0	Per 8		90	0.12	0.19	EM
<i>Epilobium montanum/tetragonum</i>	CSR	0.33	0.33	0.33	Per 6.5		95.5	0.11	0.16	-
<i>Epilobium parviflorum</i>	CSR	0.33	0.33	0.33	Per 9		90	0.11	0.22	-
<i>Equisetum arvense</i>	CR	0.5	0	0.5	Per 6		-	-	-	-
<i>Equisetum fluviatile</i>	SC	0.5	0.5	0	Per 10		-	-	-	EM
<i>Equisetum palustre</i>	CR/CSR	0.42	0.17	0.42	Per 8		-	-	-	EM
<i>Eupatorium cannabinum</i>	C/CSR	0.67	0.17	0.17	Per 8		-	0.31	0.6	-
<i>Festuca arundinacea</i>	CSR	0.33	0.33	0.33	Per 6		-	1.26	3.01	-
<i>Festuca filiformis</i>	-	-	-	-	Per 4		76.5	0.28	1.93	-
<i>Festuca gigantea</i>	CSR	0.33	0.33	0.33	Per 6		-	3.12	3.52	-
<i>Festuca pratensis</i>	CSR	0.33	0.33	0.33	Per 6		18	1.53	2.89	-
<i>Festuca rubra</i>	CSR	0.33	0.33	0.33	Per 5		-	0.79	2.75	-
<i>Filipendula ulmaria</i>	C/SC	0.75	0.25	0	Per 8		83	0.87	2.15	-
<i>Galium aparine</i>	CR	0.5	0	0.5	Ann 6		-	8.36	4.23	-
<i>Galium palustre</i>	CR/CSR	0.42	0.17	0.42	Per 9		-	0.91	3.59	EM
<i>Glechoma hederacea</i>	CSR	0.33	0.33	0.33	Per 6		-	0.69	-	-
<i>Glyceria fluitans</i>	CR	0.5	0	0.5	Per 10		-	1.2	3.37	EM
<i>Glyceria maxima</i>	C	1	0	0	Per 10		36.5	-	-	EM
<i>Gnaphalium luteo-album</i>	-	-	-	-	- 7		-	-	0.26	-
<i>Gnaphalium uliginosum</i>	R	0	0	1	Ann 6		100	0.01	0.26	EM
<i>Holcus lanatus</i>	CSR	0.33	0.33	0.33	Per 6		46.5	0.33	1.56	-
<i>Holcus mollis</i>	C/CSR	0.67	0.17	0.17	Per 6		1	0.33	1.83	-
<i>Hydrocharis morsus-ranae</i>	-	-	-	-	Per 11		-	-	-	FL
<i>Hypochaeris radicata</i>	CSR	0.33	0.33	0.33	Per 4		86.9	0.95	0.49	-
<i>Iris pseudacorus</i>	C/SC	0.75	0.25	0	Per 9		100	47.6	4.34	EM
<i>Isolepis setacea</i>	CSR	0.33	0.33	0.33	- 9		-	-	1.75	-
<i>Juncus acutiflorus</i>	SC	0.5	0.5	0	Per 8		100	0.01	1.16	-

Table A5.2.3 continued

species	CSR class	C score	S score	R score	Life span	Ellenberg F	Buoyancy (% floating after 1 week)	Seed mass (mg)	Terminal velocity (m s ⁻¹)	In-stream growth form
<i>Juncus articulatus</i>	CSR	0.33	0.33	0.33	Per 9	9	99	0.02	1.3	EM
<i>Juncus bufonius</i>	R/SR	0	0.25	0.75	Ann 7	7	-	0.02	1.64	EM
<i>Juncus conglomeratus</i>	C/SC	0.75	0.25	0	Per 7	7	99	0.02	0.95	-
<i>Juncus effusus</i>	C/SC	0.75	0.25	0	Per 7	7	60.5	0.02	1.47	EM
<i>Lemna minor</i>	CR	0.5	0	0.5	Per 11	11	-	-	-	FL
<i>Lemna trisulca</i>	SR	0	0.5	0.5	Per 12	12	-	-	-	FL
<i>Lolium perenne</i>	CR/CSR	0.42	0.17	0.42	Per 5	5	-	1.98	2.73	-
<i>Lotus pedunculatus</i>	C/CSR	0.67	0.17	0.17	Per 8	8	39	0.48	3.43	-
<i>Lycopus europaeus</i>	CR	0.5	0	0.5	Per 8	8	100	0.24	1.94	EM
<i>Lysimachia nummularia</i>	CSR	0.33	0.33	0.33	Per 7	7	100	-	-	EM
<i>Lysimachia vulgaris</i>	C/SC	0.75	0.25	0	Per 9	9	-	0.35	2.7	-
<i>Lythrum salicaria</i>	C/CSR	0.67	0.17	0.17	Per 9	9	-	0.1	1.61	EM
<i>Matricaria chamomilla</i>	R	0	0	1	Ann 5	5	-	0.05	1.71	-
<i>Mentha aquatica</i>	C/CR	0.75	0	0.25	Per 8	8	-	0.12	1.91	EM
<i>Myosotis laxa ssp cespitosa</i>	R/CR	0.25	0	0.75	Ann 9	9	-	-	-	-
<i>Myosotis scorpioides</i>	CR	0.5	0	0.5	Per 9	9	-	0.28	2.44	EM
<i>Myriophyllum spicatum</i>	CSR	0.33	0.33	0.33	-	12	-	1.49	-	SFL
<i>Nasturtium officinale</i>	CR	0.5	0	0.5	Per 10	10	0.63	0.19	2.53	EM
<i>Nuphar lutea</i>	C/CSR	0.67	0.17	0.17	Per 11	11	-	36.8	-	FL
<i>Nymphoides peltata</i>	CSR	0.33	0.33	0.33	-	11	-	-	-	-
<i>Oenanthe aquatica</i>	CR	0.5	0	0.5	Per 10	10	-	-	3.92	EM
<i>Persicaria amphibia</i>	CR	0.5	0	0.5	Per 10	10	-	4.23	-	EM
<i>Persicaria lapathifolia</i>	R/CR	0.25	0	0.75	Ann 6	6	-	2.25	-	-
<i>Persicaria maculosa</i>	R	0	0	1	Ann 6	6	-	2.12	3.46	EM
<i>Phalaris arundinacea</i>	C	1	0	0	Per 8	8	100	0.49	2.51	EM
<i>Phleum pratense ssp pratense</i>	CSR	0.33	0.33	0.33	Per 5	5	-	0.45	2.61	EM
<i>Phragmites australis</i>	C	1	0	0	Per 10	10	99.5	0.14	0.19	EM
<i>Plantago lanceolata</i>	CSR	0.33	0.33	0.33	Per 5	5	5.75	1.82	3.48	-
<i>Plantago major ssp major</i>	R/CSR	0.17	0.17	0.67	Per 5	5	3	0.25	2.55	-
<i>Poa annua</i>	R	0	0	1	Ann 5	5	-	0.25	2.16	EM
<i>Poa pratensis</i>	CSR	0.33	0.33	0.33	Per 5	5	-	0.27	2.13	-
<i>Poa trivialis</i>	CR/CSR	0.42	0.17	0.42	Per 6	6	-	0.16	1.82	EM
<i>Potamogeton alpinus</i>	CR	0.5	0	0.5	Per 12	12	93.5	1.56	3.06	SBL
<i>Potamogeton crispus</i>	CR	0.5	0	0.5	Per 12	12	-	-	-	SBL
<i>Potamogeton natans</i>	C/SC	0.75	0.25	0	Per 11	11	-	5.75	3.95	FL
<i>Potamogeton pusillus</i>	R	0	0	1	Per 12	12	-	-	-	SFL
<i>Ranunculus peltatus</i>	R/CSR	0.17	0.17	0.67	-	11	-	0.25	-	SFL
<i>Ranunculus repens</i>	CR	0.5	0	0.5	Per 7	7	82.3	2.12	3.16	EM
<i>Ranunculus repens/sceleratus</i>	CR_R	0.25	0	0.75	-	7.5	82.3	1.12	2.66	-
<i>Ranunculus sceleratus</i>	R	0	0	1	Ann 8	8	-	0.12	2.16	EM

Table A5.2.3 continued

species	CSR class	C score	S score	R score	Life span	Ellenberg F	Buoyancy (% floating after 1 week)	Seed mass (mg)	Terminal velocity (m s ⁻¹)	In-stream growth form
<i>Rorippa amphibia</i>	C/CR	0.75	0	0.25	Per	10	-	-	-	EM
<i>Rorippa palustris</i>	R	0	0	1	Ann	8	98.4	0.05	1.31	EM
<i>Rumex acetosa</i>	CSR	0.33	0.33	0.33	Per	5	-	0.84	2.09	EM
<i>Rumex acetosella</i>	SR/CSR	0.17	0.42	0.42	Per	5	95	0.34	2.9	-
<i>Rumex hydrolapathum</i>	C/CR	0.75	0	0.25	Per	10	66	3.8	2.72	EM
<i>Rumex obtusifolius</i>	CR	0.5	0	0.5	Per	5	-	1.1	2.58	-
<i>Sagina procumbens</i>	R/CSR	0.17	0.17	0.67	Per	6	57.5	0.01	0.9	-
<i>Sagittaria sagittifolia</i>	CR	0.5	0	0.5	Per	11	62	1.5	1.62	SBL
<i>Salix alba</i>	-	-	-	-	Per	7	-	-	-	-
<i>Salix caprea</i>	-	-	-	-	Per	7	-	0.08	0.13	-
<i>Salix caprea/cinerea/reichtardii</i>	-	-	-	-	Per	7.5	83.3	0.09	0.13	-
<i>Salix fragilis/alba x fragilis</i>	C	1	0	0	Per	8	84	-	0.19	-
<i>Salix viminalis</i>	C/SC	0.75	0.25	0	Per	8	-	-	0.16	-
<i>Schoenoplectus lacustris</i>	SC	0.5	0.5	0	Per	11	-	1.82	-	EM
<i>Scirpus sylvaticus</i>	C/SC	0.75	0.25	0	Per	8	100	0.12	1.6	EM
<i>Scutellaria galericulata</i>	CR/CSR	0.42	0.17	0.42	Per	8	59	0.65	-	EM
<i>Senecio vulgaris</i>	R	0	0	1	Ann	5	-	0.26	0.36	-
<i>Solanum dulcamara</i>	C/CSR	0.67	0.17	0.17	Per	8	7.5	1.43	3.12	EM
<i>Sonchus arvensis</i>	CR	0.5	0	0.5	Per	6	38.3	1.19	0.64	-
<i>Sparganium emersum</i>	CR	0.5	0	0.5	Per	11	-	4.31	-	SBL
<i>Sparganium erectum</i>	C/CR	0.75	0	0.25	Per	10	-	13.1	3.86	EM
<i>Spirodela polyrhiza</i>	R	0	0	1	-	11	-	-	-	FL
<i>Stellaria holostea</i>	CSR	0.33	0.33	0.33	Per	5	-	2.92	3.79	-
<i>Stellaria media</i>	R	0	0	1	Ann	5	4	0.36	2.95	-
<i>Symphytum officinale</i>	C/CR	0.75	0	0.25	Per	7	-	-	4.52	-
<i>Tanacetum vulgare</i>	C/CR	0.75	0	0.25	Per	6	-	0.14	2.33	-
<i>Taraxacum officinale</i>	R/CSR	0.17	0.17	0.67	Per	5	-	0.64	0.61	-
<i>Trifolium repens</i>	CR/CSR	0.42	0.17	0.42	Per	5	15.3	0.75	3.1	EM
<i>Tripleurospermum maritimum</i>	R	0	0	1	Ann	5	-	-	-	-
<i>Typha latifolia</i>	C	1	0	0	Per	10	99	0.05	0.11	EM
<i>Urtica dioica</i>	C	1	0	0	Per	6	47.7	0.21	2.44	EM
<i>Veronica anagallis-aquatica</i>	R/CSR	0.17	0.17	0.67	Per	10	89	0.04	1.29	EM
<i>Veronica catenata</i>	R/CSR	0.17	0.17	0.67	-	10	-	0.03	1.18	-
<i>Vicia cracca</i>	C/CSR	0.67	0.17	0.17	Per	6	34.5	18.8	4.43	-
<i>Vulpia bromoides</i>	SR	0	0.5	0.5	-	4	-	0.3	3.82	-
<i>Zannichellia palustris</i>	CR	0.5	0	0.5	Per	12	-	0.32	-	SFL

*Cerastium sp**: *Cerastium arvense/fontanum/glomeratum/semidecandrum* (SR/CSR_R/CSR_R/SR_SR)

*Cardamine sp**: *Cardamine amara/flexuosa/hirsuta/pratensis* (CR_R/SR_SR_R/CSR)

Appendix A5.3 Statistical tests

Table A5.3.1. Forward selections of fixed effects in poisson or binomial GLMMs, explaining number of species, in-stream growth forms presences and species number and beta diversity of the riparian vegetation by the categorical variable restoration (Rest), the continuous variable water level (Wl; exponential or quadratic when significantly better than linear, indicated in superscript with 'E' and 'Q'), and their interaction (Rest + Wl + Rest:Wl). Best models, with at least 2 units AIC decrease for addition of a variable, are underlined and in bold. Explained variance for the best models were given (marginal R²). Transects were included in all models as random effect (intercept).

	None	Rest	Wl	Rest + Wl	Rest + Wl + Rest:Wl	R ² best model
Species number						
In-stream veg	11571.0	11332.8	11327.2 ^Q	11307.9 ^Q	<u>11230.7</u> ^Q	0.15
Riparian veg	834.4	821.3	726.5 ^Q	<u>707.7</u> ^Q	711.0 ^Q	0.59
Growth forms pres						
Trailing	<u>166.5</u>	165.5	165.9	167.3	167.5	0
SFL	1731.1	1732.6	1576.8 ^Q	1577.3 ^Q	<u>1569.1</u> ^Q	0.06
SBL	4245.1	4247.1	4078.3 ^Q	4076.5 ^Q	<u>4069.7</u> ^Q	0.07
EM	3691.7	3692.0	2280.3 ^E	2247.4 ^E	<u>2221.2</u> ^Q	0.56
FL	2130.4	2102.0	2132.4	2103.9	<u>1966.4</u> ^Q	0.26
Growth forms #sp						
Trailing	<u>226.5</u>	227.0	227.2	228.1	228.0	0
SFL	2651.6	2653.0	2548.4 ^Q	2548.9 ^Q	<u>2544.0</u> ^Q	0.04
SBL	7658.9	7660.2	7465.7 ^Q	7457.1 ^Q	<u>7440.4</u> ^Q	0.12
EM	7101.3	7086.6	4952.8	4948.2	<u>4756.5</u> ^Q	0.68
FL	5334.0	5297.3	5328.6 ^Q	5294.6 ^Q	<u>5220.1</u> ^Q	0.21
Beta diversity						
Beta div OBS	334.6	295.5	288.0	<u>229.4</u>	231.4	0.59
Beta div NULL	185.5	<u>171.4</u>	-	-	-	0.21
Beta div DEV	456.7	452.6	420.6	<u>414.8</u>	414.5	0.15



Chapter 6

Synthesis

PLANT SPECIES DISTRIBUTIONS AND BIODIVERSITY ALONG STREAM RIPARIAN GRADIENTS

This thesis aimed at identifying the most important drivers of plant species distribution and diversity patterns along streams and their riparian zones, as an example of dynamic habitats with a high habitat heterogeneity and a high biodiversity. Particularly the role of dispersal versus environmental filtering, and the role of early recruitment stages (germination, seedling survival and seedling growth) during environmental filtering were investigated. The study focused on restored stream riparian zones that were excavated to bare substrate upon restoration. These bare conditions made it possible to study patterns in the initial arrival of seeds, and relate these patterns, in comparison to experimentally quantified patterns in recruitment, to adult distribution patterns in the early successional vegetation. To assess the ecological response to innovative stream restoration, the vegetation of restored and nearby unrestored reaches was compared 2 years after restoration.

The role of dispersal filtering in community assembly along stream riparian gradients

Monitoring of natural seed rain revealed clear patterns in initial seed arrival along the restored riparian gradients (Chapter 2). The arriving number of seeds and species both showed a peak around the average water line, which was caused by the deposition of high numbers of floating seeds (particularly of long-floating seeds; Nilsson *et al.* 2002) entrapped in vegetation or left behind following receding water levels (Merritt & Wohl 2002; Chambert & James 2009). Further upslope the number of hydrochorous seeds gradually decreased, reflecting the decreasing flooding frequency and duration. Across the floodplain, seeds with lower specific weights were dominantly deposited at higher elevations, probably due to their lower settling velocities in the water column, which promotes their deposition at further distance from the channel during floods analogous to particle sorting during mineral sediment deposition (Dietrich 1982; Gurnell 2007; Chambert & James 2009; Poulsen *et al.* 2014).

The observed patterns in seed deposition suggested an important role of dispersal filtering in community assembly along restored riparian gradients. Interestingly, species-specific patterns in arrival showed a very high resemblance to adult distribution patterns in the early successional vegetation. The relation with adult distribution patterns was clearly stronger than for the experimentally quantified germination, seedling survival and seedling growth, confirming that dispersal filtering dominated at least the early distribution patterns of individual plant species, and that environmental filtering was of secondary importance (Chapter 4). This was unexpected as strong environmental filtering has widely been demonstrated

along stream riparian zones, invoked by the steep moisture gradients and flooding disturbances (Keddy & Ellis 1985; Squirres & van der Valk 1992; Hölzel & Otte 2003; Van Eck *et al.* 2004; Kotowski *et al.* 2010; Garssen *et al.* 2014, 2015; Chapter 3). This unexpected result may be explained by the arrival of seeds of many species at suitable sites for establishment which were still bare and unoccupied.

Strikingly, subsequent analysis of community patterns revealed that seed arrival already foreshadowed patterns in the vegetation, with species with adult optima at wetter conditions dominating seed arrival at low elevations along the riparian gradient, and species with drier optima dominating the arrived seed community higher up. Such patterns of seed dispersal to sites suitable for establishment and growth are more commonly known from highly specialized animal-mediated dispersal syndromes like frugivorous birds that disperse seeds to optimal sites for establishment (Wenny 2001; Spiegel & Nathan 2007). Only Seiwa *et al.* (2008) and Merritt & Wohl (2002) argued that directed dispersal may be relevant to riparian vegetation patterns, as the highly buoyant seeds of willow species were disproportionately dispersed to microsites suitable for establishment, and seeds were systematically sorted into specific types of fluvial environments in a flume study. Although at this point it remains speculative, interspecific differences in seed buoyancies may have shaped the patterns of seed arrival to suitable sites for establishment observed in the present study, with very low seed buoyancies (common for many aquatic plant species; Boedeltje *et al.* 2003) promoting deposition under water (Coops & Van der Velde 1995), and very high seed buoyancies promoting deposition around the water line (Nilsson *et al.* 2002), or in drift lines high on the banks (Vogt *et al.* 2006, 2007). The exact mechanisms behind these patterns provide an interesting avenue for future research. Taking into account the dispersal of plant fragments would form a valuable addition to the study approach (Boedeltje *et al.* 2004), which in the present study may have underestimated species arrival of particularly aquatic plant species.

The unexpected strong role of dispersal filtering could also partly be explained by the low interspecific competition that prevailed in the first years after restoration activities. When a more closed vegetation will have been formed, species interactions are likely to significantly narrow down niche ranges (Pickett & Bazzaz 1978; Silvertown *et al.* 1999, 2015), which will enforce the role of environmental filtering. However, successional setbacks by flooding disturbances are a characteristic feature of stream riparian zones. This suggests that also in developed vegetations, an important role for dispersal filtering to species distribution patterns along riparian gradients will be retained. The intensity of disturbance is then likely to determine the relative importance of dispersal filtering. Also in other habitats in which disturbances set back succession, such prominent roles of dispersal filtering may be expected, which stresses the necessity of taking into account source populations, dispersal pathways

and mechanisms determining distribution patterns of propagules for the conservation and restoration of these often highly diverse ecosystems.

The role of (early-stage) environmental filtering in community assembly along stream riparian gradients

Besides dispersal filtering, strong environmental filtering occurred along the riparian gradients at the seed germination, seedling survival and growth stages (Chapter 3, 4). All three early recruitment stages showed severe limitations by abiotic stress at the wetter end of the gradient. Moreover, germination was strongly reduced at the dry end of the gradient, and for some species survival and growth were reduced by low water availability. The patterns at the wetter end of the gradient were likely caused by stress imposed by flooding, i.e. anoxic conditions, reduced availability of light and carbon dioxide, and burial of seeds, which may hamper germination, inhibit growth and cause plant senescence (Colmer & Voesenek 2009; Burmeier *et al.* 2010; Fraser *et al.* 2014). Additionally, waterlogging may have increased fungal mortality of seeds (Schafer & Kotanen 2003) and reduced survival and growth by accumulation of substances toxic to plants (Colmer & Voesenek 2009). At the dry end of the gradient, low water availability reduced recruitment by hampering seed imbibition (Evans & Etherington 1990), and by leading to seedling mortality (Grime & Curtis 1976) and suppressed growth (Haugland & Froud-Williams 1999).

Environmental variables unrelated to the hydrological gradient did not play a substantial role in environmental filtering along the riparian gradients. For a few species, recruitment was slightly increased by higher soil organic matter contents, which was probably related to the increased soil water-holding capacity (Haugland & Froud-Williams 1999), beneficial for species with higher moisture requirements (Evans & Etherington 1991). Additionally, high N and P availability stimulated recruitment of some species, as has been shown previously for germination (Peterson & Bazzaz 1978) and growth (Güsewell 2004). Altogether, water level was the main environmental filter limiting species distributions across riparian gradients of the lowland sandy streams studied. Nutrient-related environmental filtering may however increase in importance in later successional states, when biotic interactions will increase.

Although these strong effects of environmental filtering were less clear for species with distribution patterns governed by dispersal filtering, community patterns along the riparian gradient were clearly dominated by environmental filtering, particularly during the stages of seedling survival and growth, with a major role for flooding. Under flooded conditions, seed deposition showed the highest diversity but the diversity of the vegetation was strongly reduced, emphasizing the strong role of environmental filtering under harsh environmental conditions (Chase 2007; Lepori

& Malmqvist 2009). Dry conditions played a less important role for environmental filtering during seedling survival and growth in this study. Soil moisture contents of the driest plots were constantly higher than the critical 15% which was found to suppress growth of grassland species (Haugland & Froud-Williams 1999). Hence, drought stress may not be a severe limitation for riparian plant species in an Atlantic climate, such as in north-west Europe. However, expected increases in summer droughts due to climate change may increase the impact of this filter for riparian vegetation in the future (Garssen *et al.* 2014).

Interestingly, environmental filtering during all three recruitment stages was clearly species-specific, inducing species segregation along the hydrological gradient. These recruitment niches showed strong relations with indicator values that are based on adult habitat preferences (Chapter 3), and correlated strongly with patterns of species sorting along the riparian gradients in the early successional communities (Chapter 4). This demonstrated that environmental filtering already initiated niche segregation during the three early recruitment stages (Fig 6.1), and not only operates during the adult stage of the plants' life cycle, e.g. through competitive interactions (Wedin & Tilman 1993). Such effects have hardly been reported yet for recruitment processes in a field setting (but see Lenssen *et al.* 1999). Selective recruitment along hydrological gradients corresponding to adult distribution patterns has been previously reported in greenhouse studies (Keddy & Ellis 1985; Evans & Etherington 1990, 1991) and along stagnant water systems (Sarneel *et al.* 2014b). My results suggest a wider applicability of the importance of recruitment stages for vegetation patterns across hydrological gradients.

To conclude, my results demonstrated that early recruitment stages and even dispersal filtering already contribute to hydrological niche segregation (Silvertown *et al.* 2015) along riparian gradients, independently of possible further strengthening of the environmental filtering during later interspecific competition (Wisheu & Keddy 1992). As such, this stresses the necessity of considering both dispersal filtering and (early-stage) environmental filtering in studies and models on community assembly (Tilman 2004; Gravel *et al.* 2006; Adler *et al.* 2007).



Figure 6.1. Patterns in seed arrival and recruitment already initiated a gradient in the vegetation along the stream riparian gradient, while effects of interspecific competition were still very limited. Picture of the Kleine Aa site.

EFFECTS OF RESTORATION ON IN-STREAM AND RIPARIAN VEGETATION

Responses of plant species and diversity to innovative stream valley restoration

The hydrogeomorphic ‘stream valley restoration’ (Chapter 1, Chapter 5) successfully achieved the common restoration goals of increasing in-stream and riparian habitat heterogeneity (Pedersen *et al.* 2006, 2007; Lorenz *et al.* 2012; Eekhout *et al.* 2015). Reduction of the channel dimensions and widening of the riparian zones led to increased flow velocities in-stream, and to increased flooding frequency accompanied by enhanced propagule arrival (Nilsson *et al.* 2010; Chapter 2) in the riparian zones. These higher flow velocities interacted with meandering and vegetation, promoting spatial variation in flow velocities and concomitant patterns in erosion and sedimentation (Haslam 1978). This stimulated flow and depth variability and the formation of bare sand banks at the land-water interface open for pioneer colonization. Compared to conventional lowland stream restoration, more intense hydrological dynamics and wider environmental gradients were created (Fig. 6.2).



Figure 6.2. Pictures of an innovatively restored reach at the study location the Hagemolenbeek with strongly reduced (narrower and shallower) channel dimensions, meandering of the watercourse, and wider, more gradually sloping riparian zones. This restored higher flow velocities during base flow periods (picture left) and provided space for inundation during periods of high rainfall (picture right).

The increased flooding and habitat heterogeneity led to a higher diversity of riparian plant species and a higher in-stream plant diversity in the shallow water habitat near the channel margins. As this increase in diversity was much stronger at the channel margins and in the floodplains than at higher elevations in the riparian zone, which was consistent at all study locations, this strongly indicated that the hydrological dynamics triggered this vegetation response. More specifically, this could be attributed to the increased propagule arrival by flooding, to the impact of the flooding disturbances which stimulated coexistence of pioneers and competitors, and to the creation of new habitats like bare sand banks at the land-water interface which were absent at unrestored reaches (Biggs *et al.* 1998; Baattrup-Pedersen *et al.* 2000; Clarke & Wharton 2000; Rohde *et al.* 2005; Pedersen *et al.* 2006; Helfield *et al.* 2007; Jähnig *et al.* 2009; Januschke *et al.* 2011, 2014; Lorenz *et al.* 2012; Hering *et al.* 2015). Emergent plants benefitting from the bare sand-banks at the land-water interface subsequently expanded towards the shallow areas at the channel margins. This important pathway of in-stream vegetation colonization likely stimulated the diversity increase in this part of the in-stream environment (Henry & Amoros 1996). Habitat increment of the shallow water habitats probably also stimulated diversity in this zone (Biggs *et al.* 2001; Pedersen *et al.* 2006, 2007; Baart *et al.* 2010; Lorenz *et al.* 2012).

The higher flow velocities in the restored reaches resulted in a sharp decrease in floating-leaved species and an increase in trailing species (species rooting in the bank but trailing over the water). This shift in growth-form dominance indicated that more typically lotic in-stream plant communities developed at the restored reaches according to the growth form classification by Harvey *et al.* (2008). This showed that

relatively modest flow velocities of 0.16 m s^{-1} were already effective in stimulating more rheophilic plant communities, where other studies reported similar results at higher flow velocities (approximately 0.4 m s^{-1} ; Meyer *et al.* 2013, or 0.24 m s^{-1} ; Pedersen *et al.* 2006). Additionally, the higher flow velocities slowed down colonization of in-stream vegetation, as high flow velocities bring about a lower propagule retention (Riis 2008) and a diminished establishment of seedlings by promoting plant breakage or uprooting (Riis & Biggs 2003).

In addition to the effects of restored hydrological dynamics, habitat widening also showed a strong effect on the vegetation. A significantly increased species turnover along the riparian gradient (beta diversity) showed that widening opened up hydrological niches (see Silvertown *et al.* 1999, 2015) on the floodplain of the restored reaches, which apparently hardly existed at unrestored reaches. To my knowledge, this is the first study where a higher beta diversity along restored stream riparian gradients was found to be related with the increased riparian area. Previous studies that investigated riparian zone widening also reported positive effects, but these effects mainly applied to the land-water interface (Hering *et al.* 2015), or were likely caused by the excavation of pools within the widened riparian zones (Clarke & Wharton 2000). Separate analyses of functional groups (based on Ellenberg F-values) revealed that wetland species (Ellenberg F7-10) clearly increased in diversity by restoration at the increased areas of moist soils. This agrees with an important role for environmental filtering along hydrological gradients, which also explains the absence of aquatic species in these zones, as they die quickly if their environment desiccates (Haslam 1978). However, besides wetland species, also several upland species (Ellenberg F 4-6) benefitted from the widened area of wet soils in the riparian zone, which contrasts with their optimal habitat conditions. Probably the lack of competition allowed these upland species to co-occur with wetland species, while they will be competitively displaced to the drier ends of the gradients when interspecific competition increases (Pickett & Bazzaz 1978; Wisheu & Keddy 1992; Silvertown *et al.* 1999).

It is important to note that the vegetation responses described above were all short-term responses to the restoration. Especially in-stream vegetation was still clearly underdeveloped, and more permanent vegetation responses to the increased flow are yet to be evaluated. Moreover, increases in biotic interactions may, particularly in the riparian zone, lead to a decrease in alpha diversity again (Noon 1996), including the diversity among wetland species. Although flooding disturbances invoke successional setbacks, it is still uncertain if the increased flooding disturbances by the new inundation regime will be sufficient to reduce space preemption by competitors in later successional stages, and therewith retain the higher beta diversity. Promising results were reported in earlier studies where increases in pioneer species after restoration could be maintained when flow dynamics were strong enough to maintain

rejuvenation (Rohde *et al.* 2005; Januschke *et al.* 2011). Additionally to flooding disturbances, the lower nutrient availability resulting from topsoil removal at restored reaches may be beneficial for maintaining the high beta diversity, as subordinate species may have a higher chance of utilizing their niche space (e.g. Wassen *et al.* 2005). Interactions between abiotic and biotic determinants of community structure are an interesting topic for future studies on stream restoration (e.g. see Kotowski *et al.* 2010). Overall, it is clear that longer time frames are necessary to investigate the effects of increased competition and to more completely evaluate the success of the restoration measures.

Effects of dispersal limitation on restoration success

Such longer time frames are also necessary for several species to arrive at the restored reaches in the first place. Dispersal limitation has previously been shown to affect the success of conservation and restoration activities (Lindborg & Eriksson 2004; Verhoeven *et al.* 2008; Ozinga *et al.* 2009; Brederveld *et al.* 2011). Two years after restoration, diversity increase was below average at higher elevations in the riparian zone, and diversity even decreased after restoration in the central parts of the channels. Dispersal limitation most likely strongly contributed to these results, as water-borne seed deposition is low at higher elevations in the riparian zone (Chapter 2, Chapter 4), while propagules are easily washed away in-stream (Riis 2008). Significant differences in seed adaptations to long-distance dispersal (low mass, low terminal velocity, and a high buoyancy; Andersson *et al.* 2000; Soons *et al.* 2004) were observed for the vegetation at the restored reaches compared to the unrestored reaches. Although several aquatic and quite some wetland species colonized the restored reaches, more than 2 years is needed before more rare (see Baattrup-Pedersen *et al.* 2013), less well-dispersed species can reach and become established in these areas. Species accumulation has even been shown to continue up to 25 years after restoration (Hasselquist *et al.* 2015).

IMPLICATIONS FOR RESTORATION

Integrated restoration of streams and stream valleys

Combining reduced channel dimensions with a meandering watercourse and widened riparian zones was shown to be very effective in restoring in-stream flow velocities and habitat heterogeneity, and riparian niche variation. The vegetation responses showed that increased flow and stronger flooding dynamics quickly increased diversity after restoration, and that higher stream velocities led to more typically lotic in-stream plant communities. Widening of riparian zones additionally stimulated diversity by leading to a higher beta diversity, indicating that wide, gradually sloping stream valleys should

be of key importance in designing future stream restoration projects.

Based on the results in the present study, particularly combinations of these measures are recommended to maximize ecological success. Channel narrowing and shallowing can effectively increase flow velocities, but can only be applied when sufficient space for inundation is available in the stream valley for periods of high discharges. Hence, wide, extensive floodplains are necessary to moderate extremely high flow velocities that may occur during peak discharges, which may be harmful to in-stream biota. Moreover, this space is necessary for water retention to avoid flooding damage in surrounding agricultural areas. The Hagmolenbeek is a very good example of such an integrated restoration. Extremely narrowed and shallowed channels, which changed from 8.7 to 2.8 m wide, and from 0.9 to 0.4 m deep, led to increased flow velocities during base discharges and to extensive areas of flooding (>30-m wide floodplains) during higher discharges (Fig. 6.2). Besides the importance of combining measures in the stream and its valley, also the combination of reducing channel dimensions and meandering of the watercourse proved successful. The interaction between increased flow velocities and meandering of the watercourse triggered the higher flow variability and depth variability at restored reaches, and stimulated the formation of bare sand banks at the land-water interface which provided habitat for emergent pioneer species. This was clearly visible at the restored reaches of the Kleine Aa and Tungeployse beek sites where several sharp bends were constructed (Fig. 6.3). Overall, these results stress the importance of applying several restoration measures at once, focusing on the stream and its valley as whole instead of carrying out restoration measures on only specific parts of the ecosystem.

Shallow channels stimulate diversity, but caution is needed

Strongly widened instead of narrowed channels were constructed at the Hooge Raam site. This resulted in increased spatial dynamics through the formation of sand banks in-stream (Eekhout *et al.* 2013). Although diversity increased, just like it did by the increases in shallow habitats at the other sites, excessive in-stream vegetation development occurred on these sand banks at the Hooge Raam, which led to flow obstruction. This showed that overly shallow or wide channels are not favourable given the stream discharge functions. Wide and shallow channels also characterized the Luntersche beek site. Yet in-stream vegetation development remained very sparse (16% in-stream vegetation cover). It is likely that windows of opportunity for seedling establishment (Balke *et al.* 2014), were less prevalent at the Luntersche beek. Flow velocities remained higher at this study location throughout the summer period, forming a disturbance to developing seedlings by breakage or plant uprooting (Riis & Biggs 2003), or leading to limited propagule retention (Riis 2008), while at the Hooge Raam (65% in-stream cover), and also at the Hagmolenbeek (41% in-stream cover)

slower flows occurred for longer periods (personal observation). My results indicated that shallow channels are favourable for diverse in-stream vegetation communities. However, prolonged periods of stagnant water or strong water level reductions should be minimized to avoid excessive in-stream vegetation establishment. Periods of stagnant water will stimulate submerged and floating-leaved vegetation, also in deeper channels, which will increase the necessity of mowing to prevent flow obstruction. The opportunity to maintain high flow velocities throughout the growing season is strongly dependent on catchment runoff regimes. This stresses the importance of considering catchment-scale processes for successful restoration.



Figure 6.3. Pictures of the study locations with (A) sand banks at inner bends at the Kleine Aa, (B) increased vegetation establishment in inner bends at the Tungalroyse beek, (C+D) formation of in-stream sand banks which became colonized by emergent plant species at the Hooge Raam, (E) shallow and relatively wide channels at the Luntersche beek which remained sparsely vegetated in the first years after restoration, and (F) wet-dry gradients in the stream valley vegetation at the Hagmolenbeek.

Designing stream valley slopes

My results further indicate that stream valleys should be made as wide as possible, with a gradually sloping surface to meet the hydrological requirements of many individual riparian species. To favour wetland species, particularly the area in the riparian zone with average water tables between 0 and -0.3 m should be increased. It is however important to take into account soil characteristics for more specific design of riparian slopes, as soil characteristics influence capillary rise from the water table and determine moisture retention in the upper soil layers. The latter was clearly visible when comparing the Hagmolenbeek, with a more organic soil and small particle size, and the Hooge Raam, with a highly mineral soil and larger particle size. These differences in soil characteristics led to a lower capillary rise and lower moisture retention at the Hooge Raam, leading to a stronger decrease in soil moisture contents with increasingly lower water tables (Fig. 6.4). These differences in soil moisture conditions affected vegetation, as was clearly visible for germination responses of the experimentally studied riparian plant species, which showed much narrower water table niches at the Hooge Raam than at the Hagmolenbeek (Fig. 6.4). This demonstrates that stream valleys with highly mineral soils need a closer connection to the water table to stimulate wetland species, either by raising the water table more strongly, or by deeper excavation of the riparian zones.

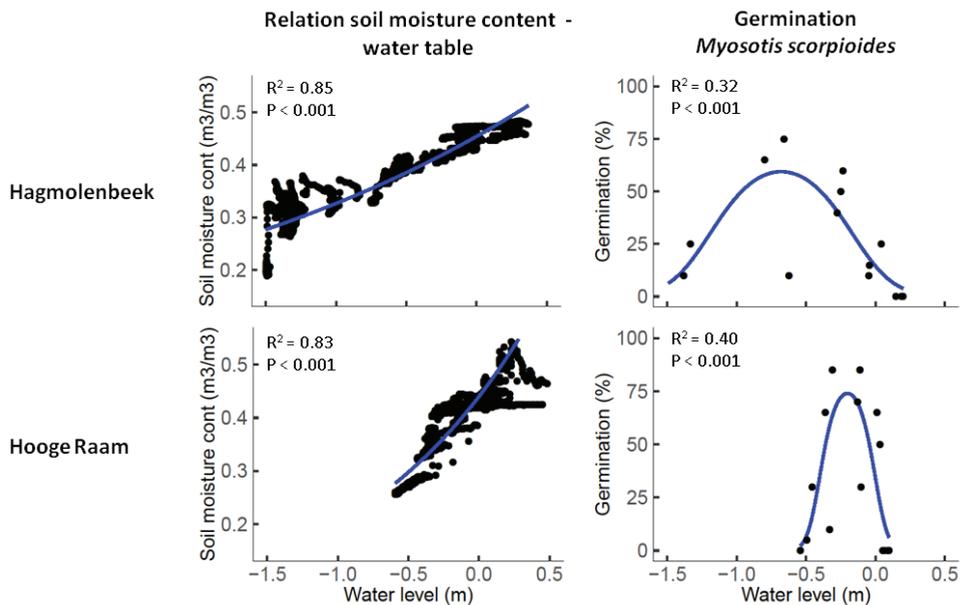


Figure 6.4. Hourly measurements of water tables and soil moisture contents in the upper soil layers of four plots along a wet-dry gradient in the riparian zone for the Hagmolenbeek and the Hooge Raam sites, measured in the period of May-August 2011 (left graphs), and experimentally quantified germination

responses of *Myosotis scorpioides* seeds along the same riparian gradients (right graphs). Negative water level values indicate that the water table lies below the soil surface; positive values indicate it is above the soil surface (flooding). Blue lines represent best model fits of linear models (left graphs) and binomial generalized linear mixed models with transects as a random effect (right graphs), with model statistics indicated in the upper left corners.

Colonization and succession of the vegetation after restoration

All study locations were allowed to colonize naturally after restoration. The results showed that this quickly happened for riparian zones where propagule arrival was stimulated by flooding. The strong influence of winter flooding for arrival of seeds of wetland species implies that the timing of restoration measures is important for success. If the excavation of streams and riparian zones takes place before the winter period many seeds will be deposited during the winter floods, enabling a quick colonization by wetland species, and giving less advantage to wind-dispersed species which dominate seed arrival in non-flooded riparian zones in summer (Moggridge *et al.* 2009). At the Haggmolenbeek site, vegetation development did not occur entirely naturally, as the riparian zones were sown with a seed mixture of *Lolium perenne*, *Trifolium repens*, and *Phleum pratense* subsp. *pratense*. Although several species managed to become established in between, this probably hampered an even greater response towards higher biodiversity and the return of wetland species. Results of the other study locations, where riparian vegetation developed quickly, showed that sowing or planting of vegetation is not necessary for minimizing erosion after restoration.

Although a quick colonization occurred and diversity increased after restoration, the species that colonized the restored reaches were mainly common species, reflecting the vegetation in the nearby catchment (Baattrup-Pedersen *et al.* 2013). This urges that landscape-level conservation and restoration planning should be carried out to optimize connectivity for target species (e.g., Verhoeven *et al.* 2008), paying specific attention to nearby seed sources. However, propagule introduction, if carried out with caution, might be an additional key measure in restoration (Hölzel & Otte 2003; Klimkowska *et al.* 2007, 2010; Van Looy 2011), especially in areas where source populations are distant. This introduction of target species should ideally be applied quickly after restoration to diminish the development of undesired species. Finally, although the increased flow and flooding regimes invoked vegetation rejuvenation locally, woody species already started to dominate at unmanaged riparian zones three years after restoration. Mowing and grazing will remain necessary unless forested streams and riparian zones are intended.

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Summary

Global habitat loss and deterioration are threatening plant diversity and associated important ecosystem functions. In order to protect sensitive species and biodiversity, a central goal in ecology is to understand the mechanisms that determine species distributions and biodiversity. Two contrasting concepts occur in this field, explaining species distributions either by species requirements and tolerances to environmental conditions (known as ‘environmental filtering’), or by patterns in the arrival of seeds and viable plant fragments, as influenced by distance to source populations and by species dispersal abilities (known as ‘dispersal filtering’).

Although both filtering processes play a role in natural plant communities, the assessment of their relative importance across time, space, or ecosystem types remains challenging. Moreover, quantitative information on the different mechanisms underlying the filtering processes is generally lacking. Environmental filtering may occur during early stages in the plant’s life cycle, such as germination or seedling survival, but also at later stages, for instance by competitive interactions among adult individuals. Dispersal filtering may occur due to a lack of nearby source populations, but also by blocked dispersal pathways, or by a mismatch in patterns of deposited seeds and suitable locations for establishment. In dynamic habitats that are prone to natural disturbances, it is particularly unclear whether environmental filtering or dispersal filtering dominates, or how the two interact. Yet, this information is of highest importance for the conservation and restoration of these ecologically valuable, but increasingly threatened habitats. When environmental filtering dominates, conservation and restoration measures should first seek to maintain or improve local environmental conditions, but when dispersal filtering dominates, it is of primary importance to protect nearby source populations and secure dispersal pathways.

Streams and their surrounding wetland areas, known as their riparian zones, provide a typical example of dynamic and highly diverse ecosystems. They are characterized by strong hydrological gradients, which promote coexistence of many different plant species that occupy their own preferred habitat along a gradient from wet (in or close to the stream) to dry conditions (further upland). Moreover, strong flooding disturbances occur that set back succession, promoting the coexistence of pioneers and competitor species. Unfortunately, streams and riparian zones have been heavily degraded worldwide due to human interventions like damming and channelization. For lowland streams, this has resulted in much wider and deeper stream channels with decreased flow velocities, and much steeper riparian zones, with strongly reduced moisture gradients, altogether decreasing habitat heterogeneity and consequently biodiversity. Despite the increasing number of restoration projects in

the past decades, ecological improvement is largely lagging behind due to landscape-scale issues such as dispersal limitation, or insufficient habitat improvement. Recently, more innovative stream restoration projects have been carried out, combining restoration of the stream and stream valley. This 'stream valley restoration' entailed the construction of narrower and shallower channels to restore higher flow velocities during base discharges, combined with meandering of the watercourse to restore spatial variability in flow and depth, and with wider and more gradually sloping stream valleys to restore space for inundation during high discharges.

This thesis aimed at identifying the most important drivers of plant species distribution and diversity patterns along lowland streams and their riparian zones, and assessing ecological responses to innovative restoration measures to provide recommendations for future restoration projects. Lowland streams generally flow through gently sloping terrain (0-5‰ slope) showing low flow velocities (0.05-0.6 m s⁻¹) with discharge patterns and flood events tightly linked to precipitation. They occur in the Pleistocene areas in the central, eastern, and southern parts of the Netherlands with soil surfaces dominantly consisting of Aeolian sand deposits. Five lowland streams were selected: the Hagmolenbeek (HM), Hooge Raam (HR), Kleine Aa (KA), Luntersche Beek (LB) and Tungelroyse beek (TR). At all locations reaches of 0.8-2 km stream length were restored according to the innovative principles described above. Only at HR, channels were widened instead of narrowed, and no meandering was applied. Streams and riparian zones were excavated to bare substrate during restoration and were allowed to colonize naturally after restoration. Only at HM, the riparian zones were sown with a grassland seed mixture to reduce possible erosion after restoration.

I combined field monitoring of seed arrival patterns along the riparian gradients of restored reaches (dispersal filtering), with field experiments on recruitment of introduced seeds and seedlings along these gradients (environmental filtering), to subsequently compare the influence of both processes on adult distribution patterns in the naturally developing vegetation. Then, the aquatic and riparian vegetation at restored reaches was compared to unrestored (still channelized) reaches, for the assessment of short-term vegetation responses to the abiotic changes brought about by the innovative restoration measures.

Chapter 2 focuses on seed arrival patterns along elevational riparian gradients. Seed traps were pinned to the ground to monitor natural seed rain along the riparian gradient at restored reaches. Identity and quantity of seeds were determined in the laboratory and, together with their trait values (such as seed buoyancy and seed specific weight) linked to the hydrological conditions at the seed traps along the riparian gradients.

Average seed numbers and species richness were significantly higher in flooded

seed traps than in non-flooded seed traps. The concentration of water-dispersed seeds gradually decreased from the channel to the upland, with a peak of highly buoyant seeds at the average water line, and elevational sorting of non-buoyant seeds within the floodplain. These results establish a critical role of water dispersal in patterns of seed deposition along the riparian gradient, and imply that natural flooding regimes form a key process to restore in riparian zones to stimulate the colonization of typical riparian species.

In **Chapter 3** the effect of local site conditions on germination, seedling survival and seedling growth of 17 native riparian plant species common to north-west Europe were quantified. Seeds and seedlings of these species were introduced across hydrological gradients in restored riparian zones and their performance was related to indicator values for adult habitat preferences regarding moisture availability.

The hydrological gradient acted as a strong environmental filter on all three recruitment processes, through imposing stress (by inundation) at low elevations and resource limitation (water shortage) at higher elevations. Other variables, such as soil organic matter content and nutrient availability, only affected recruitment marginally. Each individual plant species exhibited its own specific recruitment preference along the gradient, particularly during germination and seedling growth. These recruitment optima appeared strongly related to the preferred habitat conditions as an adult plant. This showed that strong environmental filtering during germination and seedling growth already determines later adult distributions by forming the spatial template on which all subsequent processes operate. In addition to well-known mechanisms, such as competitive exclusion at the adult stage, environmental filtering during early recruitment stages thus already strongly affects plant distribution and diversity.

Chapter 4 focuses on the relative importance of patterns in seed arrival versus patterns in environmental conditions for species distribution and diversity patterns along the hydrological gradients of restored stream riparian zones. Natural seed arrival of aquatic and riparian plants was monitored in the first year after restoration. Simultaneously, for 17 riparian plant species common to north-western Europe, patterns in germination, seedling survival and seedling growth were measured by introducing their seeds and seedlings along these gradients. Subsequently I analysed how differences in seed arrival and in germination, seedling survival and seedling growth contributed to plant species distributions in the naturally developing vegetation one and two years after restoration.

Patterns in initial seed arrival were very clearly reflected in species distribution patterns in the developing vegetation and were more important than patterns in germination, seedling survival and growth. However, environmental

filtering intensified towards the wet end of the riparian gradient, where flooding strongly reduced survival and growth of many species, inducing a wet-dry gradient in the vegetation. Strikingly, the patterns in seed arrival foreshadowed the gradient that developed in the vegetation; seeds of species with adult optima at wetter conditions dominated seed arrival at low elevations along the riparian gradient while seeds of species with drier optima arrived higher up. Thus, besides environmental filtering, these results demonstrated that non-random dispersal is an important driver of early successional riparian vegetation zonation and biodiversity patterns, a mechanism that may have been overlooked along many other environmental gradients.

In **Chapter 5** the vegetation of innovatively restored stream reaches was compared to that of nearby unrestored stream reaches. This was done by assessing physicochemical variables along complete stream valley cross-sections and evaluating the responses of aquatic and riparian vegetation, focusing on different aspects of plant species diversity.

The increased stream flow and flooding brought about by restoration resulted in a higher diversity of riparian plant species and a higher diversity of emergent pioneer species at the channel margins and the land-water interface. The higher flow velocities at the restored reaches resulted in a shift to more typically lotic (running water) in-stream plant communities, indicated by a sharp decrease in floating-leaved species and an increase in species with growth forms trailing on the water surface. Widening of the floodplain enlarged hydrological wetland niches that hardly existed at unrestored reaches, resulting in a higher species diversity especially of typical wetland plants. Although many of the colonizing species were ruderals with a high dispersal ability, and longer time-series are necessary to investigate the effects of increased interspecific competition, the combined restoration measures were very effective in restoring habitat conditions leading to distinct short-term increases in vegetation diversity of many typical stream and riparian plant species.

For future stream restoration projects, particularly combinations of reduced channel dimensions, restored meandering of the watercourse, and a widened stream valley was shown to be essential, as explained in detail in **Chapter 6**. Strong reduction of channel dimensions, required to successfully increase flow velocities during base discharges, can only be applied when sufficient space for inundation is available in the stream valley for periods of high discharges. Moreover, particularly the interaction of increased flow velocities and meandering of the watercourse triggered the increase in habitat heterogeneity at restored reaches. Increased number and area of shallow habitats strongly promoted in-stream plant diversity. However, overly wide and shallow channels may promote excessive in-stream vegetation development leading to flow obstruction. This may be moderated by maintaining high flow velocities

throughout the growing season, which requires interference in the water runoff regime at the catchment scale. Overall, these results stress the importance of applying several restoration measures at once, focusing on the stream and its valley as whole, and considering catchment-scale processes for successful restoration.

My results further indicate that wide and gradually sloping stream valleys are required to provide a sufficiently large variation in habitats for riparian plant species to realize a characteristic vegetation with high diversity. To favour wetland species, particularly the area in the riparian zone with average groundwater levels between 0 and -0.3 m should be increased. However, soil characteristics need to be taken into account as well to increase habitat diversity of riparian slopes. Porous sandy soils drain well and show low moisture retention, while clay soils or organic soils remain wet for a long time. The lower capillary rise of the ground water in highly mineral soils requires a close connection to the groundwater table to stimulate wetland species, either by ensuring a high groundwater table, or by deeper excavation of the banks.

Colonization occurred quickly at all research locations, but the critical role of winter flooding in the arrival of seeds of wetland species implies that the timing of restoration measures is important for success. Excavation of streams and riparian zones before the winter period will enable a more immediate colonization by desired wetland species, giving less advantage to wind-dispersed species which dominate seed arrival in non-flooded riparian zones in summer. The dominance of common well-dispersed species in the colonizing vegetation at the restored reaches demonstrated that landscape-level conservation and restoration planning should be carried out to optimize connectivity for target species, and that seed introduction of desired species, if carried out with caution, might be an additional key measure in restoration. Finally, although the increased flow and flooding regimes invoked vegetation rejuvenation locally, woody species already started to dominate at unmanaged riparian zones three years after restoration. Mowing and grazing will remain necessary unless forested streams and riparian zones are intended.

Nederlandse samenvatting

De biodiversiteit van planten en de daarmee samenhangende ecosysteemdiensten staan wereldwijd onder grote druk door de achteruitgang en het verdwijnen van geschikte leefmilieus. Om biodiversiteit en kwetsbare plantensoorten te kunnen beschermen is het binnen de ecologie een centraal doel om de mechanismen achter de landschappelijke verspreiding van soorten te begrijpen. Binnen dit veld bestaan twee tegengestelde concepten. Het ene concept verklaart het voorkomen van soorten aan de hand van hun eisen en toleranties ten aanzien van het milieu (ook bekend als 'milieufiltering'). Het andere concept verklaart dit voorkomen aan de hand van patronen in het neerkomen van zaden en plantfragmenten, bepaald door bijvoorbeeld de afstand tot bronpopulaties en door het vermogen van een soort zich via verspreiding van zaden en plantfragmenten te verplaatsen (bekend als 'dispersiefiltering').

Hoewel beide filteringprocessen een rol spelen in natuurlijke plantengemeenschappen, blijft het moeilijk vast te stellen wat hun relatieve belang is over de tijd, de ruimte, en over ecosysteemtypen. Daarnaast is weinig kwantitatieve informatie beschikbaar over de achterliggende mechanismen van beide filters. Zo kan milieufiltering optreden tijdens vroege ontwikkelingsstadia van een plant, zoals bij de kieming van zaden en overleving van zaailingen, maar ook tijdens latere stadia, zoals door competitieve interacties tussen volwassen planten. Dispersiefiltering kan daarnaast optreden doordat geen nabije bronpopulaties van een soort aanwezig zijn, maar ook doordat dispersieroutes zijn geblokkeerd en/of er een mismatch bestaat tussen patronen in het neerkomen van zaden en geschikte plaatsen voor vestiging van planten. Vooral in dynamische habitats welke aan natuurlijke verstoringen onderhevig zijn is het onduidelijk welke van de twee filteringprocessen domineert, of hoe ze elkaar beïnvloeden. Deze informatie is echter van groot belang voor het behoud en herstel van deze ecologisch waardevolle maar steeds sterker verstoorde habitats. Wanneer milieufiltering domineert heeft het de hoogste prioriteit om lokale milieuumstandigheden te behouden of te verbeteren, maar wanneer dispersiefiltering domineert is het vooral belangrijk om nabije bronpopulaties te beschermen en dispersieroutes veilig te stellen.

Beken en hun begeleidende moerassige oeverzones, ofwel beekdalen, zijn een typisch voorbeeld van dynamische, hoog-diverse ecosystemen. Ze worden gekenmerkt door sterke gradiënten in vochtbeschikbaarheid in de bodem. Dit stimuleert het naast elkaar voorkomen van verschillende plantensoorten omdat elke plantensoort haar eigen optimale positie kan innemen, van natte plaatsen in of vlakbij de beek tot droge plaatsen hoog op de oever. Daarnaast zorgen natuurlijke overstromingen van de oever voor een periodieke verstoring waarmee de successie van een plantengemeenschap

telkens wordt teruggezet. Dit stimuleert het naast elkaar voorkomen van pioniersoorten en competitief sterke langlevende soorten. Jammer genoeg zijn beken en oeverzones wereldwijd achteruit gegaan door menselijke ingrepen zoals afdamming en kanalisatie, ofwel het rechte trekken van watergangen. Voor Nederlandse laaglandbeken heeft dit geleid tot onnatuurlijk diepe en brede watergangen met veel lagere stroomsnelheden, en tot steilere oevers waardoor vochtgradiënten sterk in grootte zijn afgenomen. Alles bij elkaar heeft dit de variatie in habitats fors verlaagd met als gevolg een verlaging van de biodiversiteit. Ondanks het groeiende aantal beekherstelprojecten in de laatste tientallen jaren blijft ecologisch herstel vaak achter door problemen op landschapschaal zoals dispersielimitatie, maar ook door onvoldoende verbetering van leefmilieus. Recentelijk zijn innovatieve beekherstelprojecten uitgevoerd waarbij herstel van de beek werd gecombineerd met herstel van het beekdal. Dit 'beeldalbrede herstel' omvatte de aanleg van smallere en ondiepere watergangen om stroomsnelheden tijdens gemiddelde waterafvoeren te verhogen, gecombineerd met hermeandering van de watergang om ruimtelijke variatie in stroming en diepte te stimuleren, en met bredere geleidelijk oplopende oeverzones om ruimte voor overstroming te bieden tijdens hoge waterafvoeren.

Dit proefschrift richt zich op het identificeren van de belangrijkste sturende factoren in het voorkomen van plantensoorten en biodiversiteit langs laaglandbeken, en op het beoordelen van de ecologische winst na innovatieve herstelwerkzaamheden om hieruit aanbevelingen te genereren voor toekomstige herstelprojecten.

Laaglandbeken stromen over het algemeen door vlakke landschappen (helling van 0-5‰), worden gekarakteriseerd door lage stroomsnelheden (0.05-0.6 m s⁻¹) en vertonen een sterke koppeling tussen neerslag en waterafvoer. Laaglandbeken komen voor in de Pleistocene gebieden in het centrale, oostelijke en zuidelijke gedeelte van Nederland, waarvan de bovenste bodemlaag hoofdzakelijk bestaat uit Eolische zandafzettingen. Voor dit onderzoek zijn vijf laaglandbeken geselecteerd: de Hagmolenbeek (HM), Hooge Raam (HR), Kleine Aa (KA), Luntersche Beek (LB) en Tungelroyse beek (TR). Op alle locaties zijn trajecten van 0.8-2 km beeklengte gerestaureerd volgens de hierboven beschreven innovatieve uitgangspunten. Alleen bij HR is de watergang verbreed in plaats van versmald en is geen hermeandering van de watergang toegepast. De herstellende beken en oevers zijn afgegraven tot kaal zand tijdens de herstelwerkzaamheden waarna vegetatie op natuurlijke wijze kon herkoloniseren. Alleen bij HM zijn de oeverzones ingezaaid met een grasland-zadenmengsel om de bodem sneller te laten doorwortelen en zo eventuele wegspoeling van de bodem door (overstromend) beekwater te minimaliseren.

In dit onderzoek heb ik veldmonitoring uitgevoerd naar patronen in de natuurlijke afzetting van zaden langs oevergradiënten van herstellende beektrajecten

(dispersiefiltering). Tegelijkertijd heb ik veldexperimenten uitgevoerd naar kieming van geïntroduceerde zaden en naar overleving en groei van geïntroduceerde zaailingen langs deze gradiënten (milieufiltering). Aan de hand hiervan kon ik de invloed van beide filteringprocessen op patronen in het voorkomen van volwassen planten langs deze oevergradiënten evalueren. Vervolgens heb ik de beek- en oevervegetatie van gerestaureerde beektrajecten vergeleken met de vegetatie van niet gerestaureerde (nog steeds gekanaliseerde) beektrajecten. Hiermee kon ik de korte termijn respons van vegetatie op de innovatieve herstelwerkzaamheden vaststellen.

Hoofdstuk 2 richt zich op patronen in de natuurlijke afzetting van zaden langs hoogtegradiënten in de oever. Hiervoor werden zaadvallen geplaatst waarmee de aankomst van zaden langs beekoevers van herstellende beektrajecten gemonitord werd. Het materiaal uit de zaadvallen werd in het lab onderzocht op de hoeveelheid zaden en hun identiteit. Deze gegevens werden vervolgens, samen met zaadeigenschappen verkregen uit databases (zoals drijfvermogen, en het soortelijk gewicht), gerelateerd aan de hydrologische omstandigheden waarin de zaadvallen zich langs de oevergradiënten verkeerden.

Het gemiddelde aantal zaden en aantal soorten waren significant hoger in zaadvallen die door beekwater waren overstroomd dan in niet-overstroomde zaadvallen. De concentratie zaden waarvan bekend is dat ze aanpassingen hebben voor verspreiding via water nam geleidelijk af van de watergang naar hoger op de oever. Daarnaast was een piek zichtbaar van goed-drijvende zaden rond de gemiddelde waterlijn, en werden niet-drijvende zaden gesorteerd afgezet in de overstromingszone, gerelateerd aan hun soortelijk gewicht. Deze resultaten laten zien dat verspreiding via beekwater een cruciale rol speelt voor de aankomst van zaden in beekoevers, en voor patronen hierin over hoogtegradiënten langs deze oevers. Natuurlijke overstroming van beekdalen vormt daarmee een sleutelfactor voor succesvolle kolonisatie van typische oeverplantsoorten.

In **Hoofdstuk 3** is gekwantificeerd wat de effecten zijn van lokale milieuecondities op de drie kolonisatieprocessen kieming, zaailingoverleving en zaailinggroei voor 17 inheemse oeverplantsoorten die veel voorkomen in noordwest Europa. Zaden en zaailingen van deze soorten werden geïntroduceerd langs vochtgradiënten in de oevers van herstellende beektrajecten, en hun kieming, overleving en groei werden gerelateerd aan indicatorwaarden voor habitatvoorkeur als volwassen plant ten aanzien van vochtbeschikbaarheid.

De vochtgradiënt vormde een sterk milieufilter tijdens alle drie kolonisatieprocessen vanwege stress door overstroming op natte plaatsen dichtbij de beek, en door watertekort op hogere plaatsen in de oever. Andere milieufactoren zoals

de hoeveelheid organisch materiaal in de bodem beïnvloedde de kolonisatieprocessen slechts marginaal. Elke plantensoort vertoonde haar eigen voorkeursmilieu voor kolonisatie langs de oevergradiënt, vooral tijdens kieming en zaailinggroei. Deze kolonisatie optima bleken sterk gerelateerd aan de voorkeurscondities als volwassen plant. Dit toonde aan dat milieufiltering tijdens kieming en zaailinggroei al erg bepalend is voor het latere voorkomen van volwassen planten, en een ruimtelijk sjabloon vormt waarop alle vervolgprocessen opereren. Naast welbekende mechanismen zoals competitieve uitsluiting tijdens het volwassen levensstadium bepaalt milieufiltering tijdens vroege levensstadia al sterk het voorkomen van plantensoorten en daarmee de diversiteit.

Hoofdstuk 4 richt zich op het relatieve belang van patronen in de aankomst van zaden tegenover patronen in milieucondities voor het voorkomen van plantensoorten en biodiversiteit langs vochtgradiënten in herstelde beekdalen. Hiervoor zijn de natuurlijke afzetting van zaden van beek- en oeverplanten gemonitord in de eerste jaren na herstel. Tegelijkertijd zijn voor 17 veel in noordwest Europa voorkomende oeverplantsoorten, patronen in kieming, zaailingoverleving en zaailinggroei onderzocht door zaden en zaailingen te introduceren langs deze gradiënten. Vervolgens heb ik geanalyseerd hoe patronen in de aankomst van zaden en in kieming, zaailingoverleving en zaailinggroei bijdroegen aan het voorkomen van volwassen planten langs de oevergradiënten in de natuurlijk ontwikkelende vegetatie één en twee jaar na de beekherstelwerkzaamheden.

Patronen in de initiële aankomst van zaden kwamen sterk overeen met het voorkomen van volwassen planten in de zich ontwikkelende vegetatie, en waren hier belangrijker voor dan patronen in kieming, zaailingoverleving en groei. De intensiteit van milieufiltering werd echter sterker richting de natte kant van de oevergradiënt, waar zaailingoverleving en -groei van veel soorten sterk werd gereduceerd door overstroming met beekwater. Dit bracht een nat-droog gradient in de vegetatie teweeg. Opvallend genoeg vertoonde de initiële patronen in de aankomst van zaden eenzelfde nat-droog gradiënt; zaden van soorten waarvan volwassen planten een voorkeur hebben voor natte plaatsen domineerden de zaadaankomst op natte plaatsen dichtbij de beek, en zaden van soorten met een voorkeur voor drogere plaatsen waren dominant aanwezig in de zaadaankomst op hogere plaatsen in de oever. Deze resultaten laten zien dat naast milieufiltering, ook niet-random verspreiding van zaden een belangrijke sturende factor is voor vegetatiezonering en biodiversiteit patronen langs oevergradiënten; een mechanisme dat potentieel langs veel andere omgevingsgradiënten over het hoofd wordt gezien.

In **Hoofdstuk 5** is de vegetatie van innovatief herstelde beektrajecten vergeleken

met de vegetatie van nabijgelegen niet-herstelde beektrajecten. Dit is gedaan door fysisch-chemische parameters op te nemen langs complete dwarsprofielen door het beekdal en de relaties met beek- en oevervegetatie te analyseren, specifiek gericht op verschillende aspecten van plantendiversiteit.

De toegenomen stroomsnelheden en overstromingen van oevers als gevolg van het innovatieve beekherstel resulteerden in een hogere diversiteit van oeverplanten en een hogere diversiteit van emergente (onder water wortelende maar boven het water uitstekende) planten aan de randen van de watergang en op de land-water overgang. De hogere stroomsnelheden binnen de herstelde beektrajecten leidden tot een verschuiving naar meer typisch stromingsminnende plantengemeenschappen, zoals aangeduid door een sterke afname in plantensoorten met drijfbladeren en een toename in plantensoorten met een over het water kruipende groeivorm. Het verbreden van de oeverzone vergrootte de niches voor veel moerasplanten. Niches die nagenoeg niet bestonden bij de niet-herstelde steile oevers. Dit resulteerde in een hogere diversiteit van typische moerassoorten. Hoewel veel van de koloniserende soorten ruderaal betroffen (kortlevende soorten met relatief lage eisen aan het milieu en een hoge verspreidingscapaciteit), en er langere monitoring nodig is om de effecten van toegenomen competitie tussen soorten te analyseren, laten mijn resultaten zien dat de gecombineerde herstelmaatregelen zeer succesvol waren in het herstellen van milieucondities. Dit heeft geleid tot sterke korte termijn-toenames in de vegetatiediversiteit van typische beek- en oeverplantensoorten.

Voor toekomstige beekherstelprojecten is vooral de combinatie van maatregelen, te weten verkleinde beekdimensies, hermeandering van de watergang en een verbreed beekdal, van cruciaal belang, zoals in detail is beschreven in **Hoofdstuk 6**. Een sterke verkleining van de beekdimensies, nodig om stroomsnelheden succesvol te verhogen tijdens gemiddelde waterafvoeren, kan alleen maar toegepast worden wanneer voldoende ruimte beschikbaar is in het beekdal voor overstroming tijdens hogere afvoeren. Daarnaast heeft met name de interactie tussen hogere stroomsnelheden en hermeandering ervoor gezorgd dat habitatdiversiteit werd verhoogd in herstelde beektrajecten. Het toegenomen aantal en oppervlak van ondiepe habitats heeft de diversiteit van beekvegetatie sterk gestimuleerd. Te brede of te ondiepe beken kunnen echter excessieve groei van beekplanten in de hand werken met blokkades en opstuwning van water als gevolg. Excessieve groei van beekvegetatie kan tegengegaan worden wanneer stroomsnelheden hoog genoeg zijn gedurende het groeiseizoen. Om dit te bereiken zullen veelal ingrepen op stroomgebiedschaal nodig zijn ten aanzien van waterafvoer. Alles bij elkaar benadrukken deze resultaten het belang van het toepassen van meerdere herstelmaatregelen tegelijk, gericht op de beek en het beekdal als geheel, en het in acht nemen van processen op stroomgebiedschaal voor

succesvol ecologisch herstel.

Mijn resultaten laten verder zien dat brede en geleidelijk oplopende beekdalen voor de benodigde ruimte en variatie in habitats zorgen, doorslaggevend om een karakteristieke biodiverse beekdalvegetatie te realiseren. Om moerassoorten te stimuleren dient specifiek de oeverzone met grondwaterstanden tussen de 0 en -0.3 m vergroot te worden. Bodemeigenschappen dienen hierbij echter in beschouwing genomen te worden om de habitatdiversiteit van oevergradiënten te vergroten. Poreuze zandige bodems laten snel water door en drogen sneller uit, terwijl kleiachtige en organische bodems veel langer vochtig blijven. De lagere capillaire opstijging van het grondwater in minerale zandige bodems vraagt om een nauwere connectie met het grondwaterniveau om moerassoorten te stimuleren, hetgeen te bereiken is door het grondwaterniveau te verhogen of door oevers dieper af te graven.

Kolonisatie van vegetatie vond bij alle onderzoekslocaties snel plaats, maar de cruciale rol van winteroverstroming voor de aankomst van zaden van moerassoorten impliceert dat de timing van herstelwerkzaamheden belangrijk is voor succes. Wanneer graafwerkzaamheden in beken en oevers vóór de winterperiode zijn afgerond, stimuleert dat een directere kolonisatie van gewenste moerassoorten, waarbij minder voordeel wordt gegeven aan windverspreide soorten die de zaadaankomst domineren in niet-overstroomde oeverzones in de zomer. De dominantie van algemene, goedverspreidende soorten in de koloniserende vegetatie van de beekherstelprojecten laat verder zien dat een landschapsschaal benadering nodig is om connectiviteit van doelsoorten te optimaliseren, en dat introductie van gewenste soorten, wanneer voorzichtig toegepast, een toegevoegde sleutelmaatregel kan zijn voor succesvol herstel. Afsluitend is het van belang erop te wijzen dat bij beekherstelprojecten waar geen vegetatieonderhoud werd gepleegd houtige planten drie jaar na beekherstel op veel plaatsen gingen domineren. Ondanks de toegenomen lokale vegetatieverjonging als gevolg van de hogere stroomsnelheden en toegenomen overstromingen zal maaien en/of begrazen nodig blijven tenzij beboste beken en oevers beoogd zijn.

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Rob Fraaije was born on 23 August 1984, in Ammerzoden, the Netherlands, and graduated from secondary school in 's-Hertogenbosch. In 2003 he started with the study Biology at the Radboud University of Nijmegen, where he developed a strong interest in aquatic and wetland ecosystems. He chose to carry out research internships via the Aquatic Ecology & Environmental Biology group and the Animal Ecology group of the Radboud University of Nijmegen. During these internships he studied aquatic macroinvertebrates at Stichting Bargerveen, aquatic macrophytes and biogeochemistry at B-WARE Research Centre and coral reef fish at the Tanzanian Fisheries Research Institute and Carmabi Research Institute. Having become more enthusiastic for aquatic and wetland ecology, he decided to apply for a PhD position at Utrecht University, where he started in the Ecology and Biodiversity group, in 2010, under supervision of Merel Soons and Jos Verhoeven. He combined his PhD research with a role as secretary in the board of the Centre for Wetland Ecology, and worked part-time at FLORON (Floristisch Onderzoek Nederland) during the finishing of his thesis, which was submitted in March 2016. During the final two years of his PhD research he became triggered by data analysis and programming, which he now combines in his position as Data Analytics Specialist at In Summa Business Intelligence, Raamsdonksveer, the Netherlands.