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Effects of river regulation measures on floristic diversity and possibilities for its promotion in riverbank habitats along German Federal Waterways

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List of publications

This dissertation is based on the following three papers:

1. WOLLNY, J. T., OTTE, A. & HARVOLK-SCHÖNING, S. (2019): Dominance of competitors in riparian plant species composition along constructed banks of the German rivers Main and Danube. *Ecological Engineering* 127, 324-337. DOI: https://doi.org/10.1016/j.ecoleng.2018.11.013*

2. WOLLNY, J. T., OTTE, A. & HARVOLK-SCHÖNING, S. (2019): Riparian plant species composition alternates between species from standing and flowing water bodies – results of field studies upstream and downstream of weirs along the German rivers Lahn and Fulda. *Ecological Engineering* 139, 105576. DOI: https://doi.org/10.1016/j.ecoleng.2018.08.006*

3. WOLLNY, J. T., BERGMANN, W., OTTE, A. & HARVOLK-SCHÖNING, S. (submitted manuscript): River regulation matters: Riverbank vegetation is characterized by more typical riverbank plant species with growing distance to weirs – Results of field studies along the German river Lahn.

The conceptualization, data analysis and writing of all three studies were central parts of my area of responsibility. The fieldwork related to the first study and most of the fieldwork for the second study was conducted by me. Willi Bergmann supported me in data sampling for the second and third study. Carina Marx helped with sampling vegetation for the third study. All authors gave valuable comments and suggestions for the improvement of the manuscripts.

Chapter 1

Synthesis

1.1 Introduction

1.1.1 Rivers and floodplains

The original character of rivers and floodplains is defined by high habitat dynamics due to recurring flooding events that vary in seasonality, intensity and frequency (WARD 1998). Thus, these habitats are frequently subject to sediment relocations, inducing a dynamic and differentiated habitat mosaic (TOCKNER & STANFORD 2002). This habitat mosaic is further shaped by an ecological gradient that arises from the frequency and intensity of flooding events. In this way, coarse sediments are deposited close to the river, whereas finer sediments are found with growing river distance, thus accounting for a characteristic zonation of vegetation of floodplains. Nearby the river, this zonation is characterized by species from the *Bidentetea tripartiae* and *Agrostietea stoloniferae* plant communities that occur during low water phases in the summer between low and mean water line. By contrast, species from reeds of flowing waters gain in dominance above the mean water level. With growing distance to the river channel, they are gradually replaced by softwood shrubs and trees of the genus *Salix*. While softwood species can resist flooding events of medium extent and frequent recurrence, hardwood forest species like *Fraxinus excelsior*, *Ulmus glabra*, *Ulmus laevis* and *Quercus robur* are limited to areas with reduced flooding duration in more distance to the river (ELLENBERG & LEUSCHNER 2010). Consequently, floodplains act as transition zone between aquatic and terrestrial ecosystems. In concert with a high habitat heterogeneity in a very small space, they provide habitat for a broad range of specialized species that evolved over a long time, thus ranking among the most species-rich ecosystems worldwide (DÉCAMPS 2011).

Due to the linear structure of floodplains, these ecosystems perceive important functions for biotope cross-linking and are thus of high importance for animal migration (NAIMAN & DÉCAMPS 1997). Further, they fulfil important ecosystem functions such as flood and nutrient retention, carbon fixation (SCHOLZ ET AL. 2012), groundwater level regulation, sediment transport and deposition (HUPP ET AL. 2009).

1.1.2 River regulation measures

As floodplains are high productive areas with high water availability, humans used them for settlement, agriculture, industry, energy production and transportation for many years (GALIL ET AL. 2007; MALMQVIST & RUNDLE 2002), wherefore they are subject to continuous changes (STRAYER & DUDGEON 2010), which gained in intensity over time. The most intensive regulation measures along rivers were implemented during the 19th century (SCHIEMER ET AL. 1999; DEILLER ET AL. 2001). These included the construction of dikes for the limitation of floodplains to a defined space, but also measures like river straightening and the installation of embankments, impoundments and waterway channels, which were carried out to use rivers as medium for transport purposes (SCHMITT ET AL. 2018; DÉCAMPS 2011; GILLESPIE ET AL. 2015; BOOTH & JACKSON 1997).

Embankments were installed to prevent riverbank soil erosion caused by waves due to shipping traffic. These include loose stone fillings that are also known as ripraps, which are frequently found along riverbanks of large rivers nowadays (REID & CHURCH 2015; ANGRADI ET AL. 2004). As a consequence, the lateral connectivity between river and floodplain is negatively affected (DEILLER ET AL. 2001), which also applies to the natural disturbance regime by recurring flooding events and sediment dynamics, leading to reduced habitat heterogeneity in floodplains (WARD 1998). As riprap installation requires the removal of riparian vegetation (LI & EDDLEMAN 2002) and the steepening of riverbanks, the riparian transition zone is narrowed, which hampers the development of riparian vegetation. Moreover, due to their rocky structure, ripraps cause higher local temperatures along the riverbanks during summer time than under natural conditions (CAVAILLÉ ET AL. 2013), which promotes thermophilic species with reduced water demands along riverbanks. Compared to natural conditions, ripraps thus account for distinct shifts in riverbank species composition.

While ripraps perceive a relevant role in the prevention of riverbank erosion, impoundments were installed to overcome differences in the river system that are related to topography (STAMM 2006). Impoundments rank among the most frequent (PETTS 1984), but also to the most extensive river regulation measures, as they distinctly alter the river´s natural flow regime (BEJARANO ET AL. 2018a). By comparison to free-flowing rivers, impounded rivers are characterized by a dampened flooding frequency, intensity and seasonality (BUNN & ARTHINGTON 2002; POFF & ZIMMERMAN 2010), lower water flow velocities (JANSSON ET AL. 2000) and thus higher water temperatures (WEBB ET AL. 2008). Therefore, they are subject to profound negative ecosystem changes, being displayed by reductions in lateral and longitudinal connectivity, with adverse effects for migrating animals and for the river flow continuum (BUNN & ARTHINGTON 2002), causing an increasing sediment deficit in the river system (NILSSON & BERGGREN 2000).

1.1.3 Urban rivers

The river modifications described above led to a uniform appearance of today´s rivers. Therefore, the existing literature summarizes these profound river system alterations by using the term of *urban rivers* (WALSH ET AL. 2005). Most of the water discharge of urban rivers is restricted to the river channel, wherefore especially free-flowing urban rivers show higher water flow velocities (PAUL & MEYER 2001). This is mainly the case during heavy rainfalls, since water discharges from the catchment area reach the river channel fast, as the adjacent catchment areas are affected by a high sealing degree (PAUL & MEYER 2001). As a result, the water´s shear stress level in the riverbed is raised, which accounts for an ongoing riverbed erosion and led to a gradual lowering of the groundwater table, causing reduced water availability in the floodplains (GURNELL ET AL. 2007; GROFFMAN ET AL. 2003). To counter this, riverbeds are also protected by ripraps (FISCHENICH 2003).

For reasons of traffic safety, especially woody riparian vegetation is removed regularly in direct riverbank areas (ANGRADI ET AL. 2004). This induces deficits in shading along the direct riverbank areas and thus reduced water temperature differentiation in the river channel, promoting adverse effects for aquatic organisms (BROOKS ET AL. 2006). Hence, water temperatures of urban rivers are higher, resulting in a lower oxygen saturation of water than under natural conditions (PAUL & MEYER 2001).

The restriction of the river channel to a narrow also causes a reduction of the floodplain vegetation (WARD 1998), which limits the floodplain´s buffering capacity and led to increasing concentrations of nutrients and pollutants in the water over the last decades (PAUL & MEYER 2001; WALSH ET AL. 2005). As hydrological and morphological dynamics substantially determine floodplain species diversity (MALMQVIST & RUNDLE 2002), the intensive regulation measures induced essential shifts in riparian species composition, leading to a reduction of the typical vegetation zonation in riparian habitats (MERRITT & WOHL 2006).

1.1.4 Ecological status of running waters and protection programs

River regulation resulted in far-reaching consequences for the ecological status of running waters and for biodiversity of floodplains, which exhibits enormous declines (STRAYER & DUDGEON 2010). By global comparison, the density of river regulation measures is the highest along European rivers (NILSSON ET AL. 2005), underlining the direct correlation between a thriving economy and growing pressures on river ecosystems (TOCKNER & STANFORD 2002). Against the background of a growing world population and the simultaneously increasing energy demand, it is expectable that this trend will continue and will also reach river systems like the Amazon River, which to date were largely unaffected by regulation measures (ZARFL ET AL. 2015; BELLMORE ET AL. 2017). Moreover, it is expected that river regulation induced effects will be accompanied by climate change generated effects, as increasing temperatures will affect hydrology and water temperatures (NILSSON ET AL. 2013), additionally accounting for shifts in riparian species composition (FERNANDES ET AL. 2016).

As riparian ecosystems exhibit extraordinary high levels of biodiversity compared to terrestrial ecosystems, but are also affected for a major part by biodiversity declines (DUDGEON ET

AL. 2006), many protection programs were adopted for their protection. On a global scale, this is represented by the Ramsar Convention on Wetlands (UNITED NATIONS 1971), the Convention on Biodiversity (UNITED NATIONS 1992) and the Millenium Ecosystem Assessement (MILLENIUM ECOSYSTEM ASSESSMENT 2005). The Water Framework Directive (EUROPEAN PARLIAMENT 2000), the Habitats Directive for Flora and Fauna (COUNCIL OF THE EUROPEAN COMMUNITIES 1992) and the European Biodiversity Strategy (EUROPEAN COMMISSION 2011) were formulated for the protection of riparian systems as legal instruments at European level. In Germany, the Federal Programme *Blue Belt* was introduced to promote measures encompassing a higher degree of naturalness along Federal Waterways (FEDERAL MINISTRY OF TRANSPORT AND DIGITAL INFRASTRUCTURE & FEDERAL MINISTRY FOR THE ENVIRONMENT, NATURE CONSERVATION AND NUCLEAR SAFETY 2017). This should act as support for the achievement of the goals defined by the Water Framework Directive, to reach a good ecological potential along Federal Waterways until 2027 (EUROPEAN PARLIAMENT 2000). Due to regulation measures and measures related to the establishment and maintenance of infrastructure, two thirds of the original floodplain area are lost in Germany. By contrast, only 10% of the present floodplain area are in an ecological functional state (BRUNOTTE ET AL. 2009), underlining the urgent need for action in this field.

1.1.5 Objectives and study questions

Against the background of the high importance of floodplain ecosystem functions and from biodiversity perspective, promotion of a higher degree of naturalness along German Federal Waterways as urban rivers receive more attention than ever before, not least due to the Water Framework Directive and the Federal Programme *Blue Belt*. In which way this might be achieved and how the success of restoration measures can be evaluated, is the main aim of this dissertation. Due to the growing requirements from economical and ecological perspective, the interplay between involved stakeholders from economy and ecology is fraught with challenges. Thus, suggestions for measures targeting the promotion of a higher floristic diversity along Federal Waterways need to be evaluated in consideration of their purpose as medium for the transport of goods and traffic safety. As regulation measures become the most apparent along riverbanks of German Federal Waterways, this dissertation focuses on the development of restoration measures for these habitats. For the evaluation of their eligibility for urban riverbanks, the following questions were essential:

1. Which plant species are typical for riverbank vegetation along German Federal Waterways?
2. Which traits do these species have?
3. Which plant species occur rarely and which site conditions promote typical riverbank plant species or at least species with similar traits?
4. How diverse are riverbanks regarding plant species diversity and functional diversity and which site conditions favor increasing levels of species and functional diversity?
5. Which measures are applicable to promote floristic diversity along German Federal Waterways?
6. What can be concluded from this dissertation for restoration practice along German Federal Waterways?

1.2 Methods

1.2.1 German Federal Waterways

The German Federal Waterway network comprises 7300 km, whereby 3032 km are regulated by impoundments (41%). 1735 km are represented by canals (24%) and 2533 km (35%) include free-flowing sections (STAMM 2006). As Federal Waterways mainly serve for public traffic, they need to fulfil the requirements for a safe water discharge and for a safe transportation of goods (§ 8 (1) FEDERAL WATERWAY ACT). To this end, maintenance measures should ensure that flowing channels and riverbanks are undamaged and free of flow barriers (§ 8 (2, 4) FEDERAL WATERWAY ACT). As the primary Federal Waterways network (e.g. Danube, Main-Danube-Canal, Main) covers most of the shipping traffic, intensive maintenance measures are inevitable. By contrast, maintenance measures along secondary Federal Waterways (e. g. Lahn, Fulda) are limited to mowing of lockages, waterway signs and water level monitoring stations, the removal of flow barriers and improvement works of embankments (J. SCHMIDT, Federal Waterways and Shipping Administration, January 31, 2017).

1.2.2 Study areas

Data collection was carried out along selected reaches of the rivers Danube, Main (chapter 2), Lahn (chapter 3 and 4) and Fulda (chapter 3) (Fig. 1.1). The climate is subatlantic to subcontinental with an average annual temperature ranging from 8 °C to 10 °C and annual precipitations from 500 mm to 800 mm (GERMAN METEOROLOGICAL SERVICE 2017a; GERMAN METEOROLOGICAL SERVICE 2017b; GERMAN METEOROLOGICAL SERVICE 2018; HESSIAN STATE OFFICE FOR ENVIRONMENT AND GEOLOGY 2013c). The river´s water discharge regime is defined as pluvial (KOENZEN 2005). The study areas are located in the Western Hessian Mountainous and Sink Countries and the Rhenisch Slate Mountains (Lahn), the East Hessian Highlands (Fulda) (KLAUSING 1988b), the Main Franconian Plates (Main), the Bavarian Tertiary Mollasses Hills, the Iller-Lech Plates and the Danube Valley (Danube) (BAVARIAN STATE MINISTRY FOR REGIONAL DEVELOPMENT AND ENVIRONMENTAL ISSUES 1984) ranging from 98 a.sl. (Marktheidenfeld) to 313 a.s.l. (Pfatter). The prevailing soil types are fluvisols and cambisols (HESSIAN STATE OFFICE FOR ENVIRONMENT AND GEOLOGY 2013a; BAVARIAN STATE OFFICE FOR ENVIRONMENT 2017a) formed by holocene alluvial sediments (HESSIAN STATE OFFICE FOR ENVIRONMENT AND GEOLOGY 2013b; BAVARIAN STATE OFFICE FOR ENVIRONMENT 2017b).

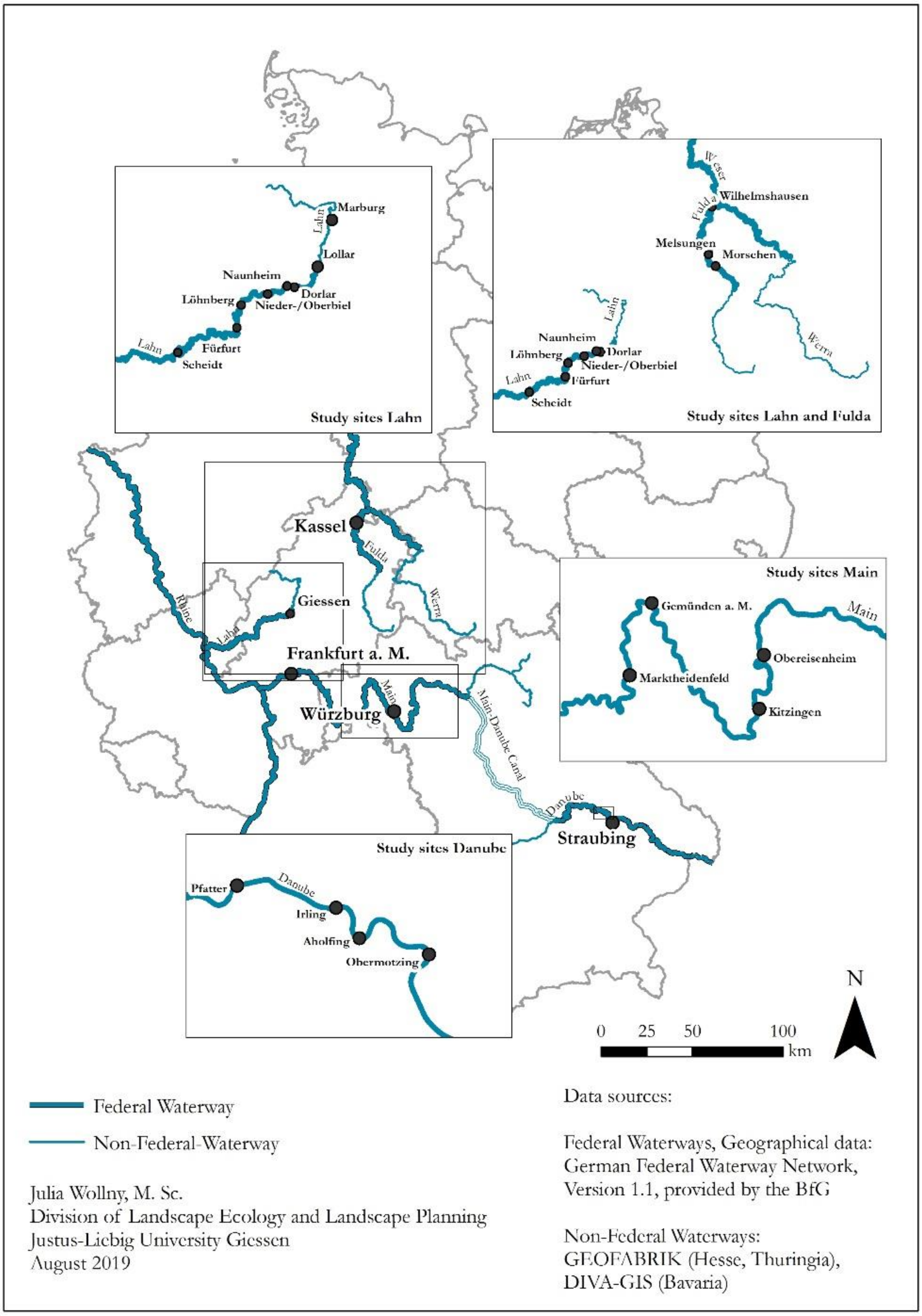

Fig. 1.1 - Location of the study areas along the Federal Waterways Main, Danube, Lahn and Fulda.

1.3 Chapter outline

The basis of this dissertation is formed by three manuscripts, which were submitted to international peer-reviewed scientific journals. The manuscripts presented in chapter 2 and 3 are already published; the study in chapter 4 was submitted and is currently under review. The studies in chapter 2 and 3 deal with the most frequently implemented river regulation measures along German Federal Waterways: the installation of ripraps (chapter 2) and impoundments (chapter 3). These manuscripts were essential for the understanding of riverbank vegetation structures along highly regulated rivers. The third study (chapter 4) was built on the conception of the second study (chapter 3). This study contributed essentially to the understanding of water level fluctuations along river stretches with high and reduced regulation intensity and their value for species composition in riverbank habitats. Accordingly, it was possible to draw conclusions in which way the success of riverbank restoration measures along intensively regulated rivers can be assessed.

In the following, the contents and the applied methods for each study are briefly introduced prior to the synthesis of the main results and conclusions of this dissertation.

Chapter 2

Dominance of competitors in riparian plant species composition along constructed banks of the German rivers Main and Danube

This manuscript deals with floristic differences of riverbanks that are structurally different between each other. The main aim of this study was to assess, which bank structure is suitable to promote effectively typical riverbank species along German Federal Waterways. To this end, vegetation was recorded along banks that were secured by ripraps and by ripraps in the waterway´s channel and along unfortified banks directly above the actual water level. The fieldwork was conducted in summer 2016 at four study sites along the river Main and at four study sites along the Danube. The dataset consisting of 94 vegetation relevés was analyzed by means of multivariate and univariate statistical approaches (non-metric multidimensional scaling, indicator species analysis, ecological and functional species traits, statistical comparison of plant and functional diversity measures) to detect the main differences in riverbank species composition between the studied bank types.

Chapter 3

Riparian plant species composition alternates between species from standing and flowing water bodies – Results of field studies upstream and downstream of weirs along the German rivers Lahn and Fulda

To assess the impact of impoundments on riverbank vegetation and to determine potential areas for riverbank restoration measures along impounded rivers, the riverbank vegetation along upstream and downstream reaches of weirs was compared. The vegetation data were collected directly above the actual water level at six weirs along the river Lahn and three weirs along the river Fulda within a maximum distance of one kilometer upstream and downstream of each weir. The fieldwork was carried out during the summers 2016 and 2017 and resulted in 144 vegetation relevés in total, as 16 relevés were collected for each weir (eight relevés upstream and eight relevés downstream; detailed information on the study design in chapter 3.2.2). The data analysis on major differences in species composition mainly followed multivariate approaches, using non-metric multidimensional scaling and indicator species analysis. Significant and not significant indicator species were analyzed regarding differences in species traits and species habitat origin.

Chapter 4

River regulation intensity matters: Riverbank vegetation is characterized by more typical riparian plant species with growing distance to weirs – Results of field studies along the German river Lahn

From riverbank restoration planning perspective, the most important finding from the study presented in chapter 3 was that downstream reaches reveal a higher probability for successful riverbank restoration measures than upstream reaches, as typical riverbank species or species with comparable traits occurred more frequently. Downstream occurrences of summer annual *Bidentetea* species also contributed to this conclusion. Nonetheless, the reasons for occurrences of summer annual plant species were not completely clear, as they are generally rare along urban rivers and strongly reliant to weather conditions. To assess, whether these species might occur more frequently along river stretches exhibiting a lower degree of regulation intensity, river stretches along the Lahn were studied that are not classified as Federal Waterway and where lockages in direct surroundings to the weirs are absent. The data basis for this study consisted of 72 vegetation relevés. 48 vegetation samplings from upstream (24 relevés) and downstream (24 relevés) river stretches were used from the data basis for the study forming chapter 3. 24 relevés displaying a lower regulation intensity were sampled during summer 2018 (detailed information on the study design in chapter 4.2.2). Data analysis was carried out by means of non-metric-multidimensional scaling, indicator species analysis, an analysis of species habitat origin based on significant and not significant species, csr-signatures and measures on plant species and functional diversity.

1.4 Main results and conclusions

1.4.1 Classification and assessment of riverbank plant species composition and plant species traits of Federal Waterways

Present state

80% of riverbanks along German Federal Waterways are protected by ripraps (L. SYMMANK, Federal Institute of Hydrology, September 25, 2017) to avoid bank erosion, occurring as a consequence of shear forces that are induced by shipping traffic (REID & CHURCH 2015). In the study areas, riverbanks were strongly inclined, as the bank steepness amounted to 24% on average (see AD-HOC-ARBEITSGRUPPE BODEN 2005), thus showing essential differences to riverbanks in their natural state and therefore to natural riverbank plant species composition. Prior to the formulation of adequate restoration measures, a description and assessment of the current state is required (PALMER ET AL. 2005), which is aimed in the following sections.

Species with medium to high water demands (Ellenberg indicator values for moisture: 5-8) and high nutrient demands (Ellenberg indicator values for nutrients: 7-9) (ELLENBERG ET AL. 1991) from the nitrophilous tall herb communities of softwood (*Convolvuletalia*; *Calystegia sepium*, *Galium aparine*) (OBERDORFER 1993, p. 137) and hardwood floodplains (*Glechometalia*; *Urtica dioica*, *Chaerophyllum aureum*) (KLIMEŠOVÁ 1994; OBERDORFER 1993, p. 157) dominated the species composition above the waterline. Further, *Impatiens glandulifera* as indicative species for flooding events and *Phalaris arundinacea* as indicative species for alternating moisture conditions were abundant (ELLENBERG ET AL. 1991). Species composition along the Danubian riverbanks was also joined by *Festuca arundinacea* as species from flooded meadows (*Agrostietea stoloniferae*), implying increased habitat dynamics due to a relatively lower bank steepness (20 ± 4%, Main: 26 ± 13%, Lahn: 23 ±18%, Fulda: 28 ± 25%).

Areas in direct water vicinity were lined by species from riparian zones that are naturally poor in woody species and by amphibian plant species like *Rorippa amphibia* or *Iris pseudacorus* (OBERDORFER 1992a, p. 156). With growing distance to the water, typical woody species from softwood forests (*Salicion albae*; *Salix alba*, *Salix viminalis*, *Salix triandra*) (OBERDORFER 1992b, p. 19) and hardwood forests (*Alno-Ulmion*; *Fraxinus excelsior*, *Acer campestre*) (ELLENBERG & LEUSCHNER 2010, pp. 448-453) grew in dominance. These species generally showed higher abundances than species from amphibian habitats. Riverbank vegetation was also characterized by species from wet grasslands (*Molinietalia caeruleae*; *Lythrum salicaria*, *Lysimachia vulgaris*) (OBERDORFER 1993, pp. 348-352) and mesic grasslands (*Arrhenatheratalia*; *Vicia cracca*, *Phleum pratense*) (OBERDORFER 1993, pp. 405-407), whereby species from wet grasslands occurred more often. Apart from the cr-strategists *Impatiens glandulifera* and *Galium aparine*, species composition was dominated by competitive species (c-strategists) from terrestrial habitats (GRIME 1979) (chapter 2).

Riverbanks in direct proximity upstream and downstream from weirs along the rivers Lahn and Fulda were represented by alternating abundances of species from standing and flowing water bodies, displaying weir-induced hydrodynamic differences in the river course. Beside from terrestrial species, upstream species composition was joined by species from swamp forests (*Alnion glutinosae*; *Alnus glutinosa*, *Filipendula ulmaria*) (OBERDORFER 1992b, pp. 34-35) and reeds of still waters (*Phragmitetum communis*; *Phragmites australis*, *Lycopus europaeus*) (OBERDORFER 1992a, p. 126). Typical species for riverbanks of free-flowing rivers like *Phalaris arundinacea* were less common upstream. These species gained in dominance along the downstream reaches, which also applies to species from flooded meadows (*Poa trivialis*; *Rumex obtusifolius*) (OBERDORFER 1993, pp. 318-320). By contrast to upstream reaches, downstream reaches may also provide habitat for summer annual species from bur-marigold and orache bank communities (*Bidentetea tripartitae*; *Erysimum cheiranthoides*, *Persicaria lapathifolia*, *Persicaria dubia*) (OBERDORFER 1993, p. 116). Nonetheless, these occurrences greatly depend on appropriate weather conditions during the vegetation period, as these species are reliant on low water levels (chapter 3 and 4). Along the Danube and the Main, these species were limited to occasional findings (Danube: *Veronica catenata*; Main: *Persicaria hydropiper*), whereby they remained absent along the Fulda. Thus, these species and consequently their traits (annuals, cr-/sr-strategy) were assessed as rare, by contrast to species from flooded meadows. These species occurred with medium frequencies in the dataset (chapter 3) and are characterized by balanced proportions of csr-, cs- and c-strategists when occurring as plant community (OBERDORFER 1993, p. 318). While c-strategists were the most dominant species type in riverbank vegetation (chapter 2), cr-strategists were restricted to riverbanks with low bank steepness, where site conditions were governed to a higher extent by alternating water levels (chapter 2). This also was true for the Lahn downstream reaches that exhibited more hydrodynamic conditions, although these sites exhibited higher bank steepness (chapter 3).

Assessment of the current state

Species composition implies distinct shifts in riverbank vegetation of German Federal Waterways. Due to recurring flooding events and alternating water levels, banks adjacent to the river are naturally free of woody vegetation. Further, they are characterized by transition zones of *Salix* shrubs to *Salix* trees with growing distance to the river channel that are clearly separable from each other (ELLENBERG & LEUSCHNER 2010, p. 430). However, the riverbank species composition also includes hardwood floodplain species and species from mesic grasslands, which implies dampened flooding events, as hardwood forest species naturally occur between mean annual flood line and flooding peaks (ELLENBERG & LEUSCHNER 2010, p. 430). Weakened hydrodynamics mainly occur due to the high bank steepness, which contributes essentially to the reduction of the active floodplain and the typical riparian zonation (NEW & XIE 2008; MERRITT & WOHL 2006). Thus, species from soft- and hardwood forest are found in direct vicinity to each other, establishing new plant communities along urban riverbanks (HARVOLK ET AL. 2014), that further provide secondary habitats for species of swamp forests and reeds of still waters (chapter 3). Moreover, occurrences of mesic grassland species and the generally high proportion of species with mesic moisture demands point to decreasing water availability in floodplains, which is also known as terrestrialization (CATFORD ET AL. 2014), nowadays an ongoing process along regulated rivers (PEDERSEN ET AL. 2006). One of the major reasons for the reduced connectivity between river and floodplain is the deepening of the riverbed, which induces sinking groundwater levels (WARD 1998). Especially along waterways with high traffic intensity like the rivers Danube and Rhine, this process is further overlapped by sparsely vegetated riverbanks that are protected by riprap. Due to their rocky structure, riprap heat up during summer, which induces local differences in climate and favours thermophilic species like *Sedum acre* (chapter 2) at sites that would naturally be defined by high water availability (CAVAILLÉ ET AL. 2013).

Furthermore, the high bank steepness results in a strong moisture gradient along riverbanks and a reduction of transition zones between water and land. Consequently, there is a decrease in suitable habitat for low competitive and small species with short lifespans and high seed production from habitats that experience frequent disturbances by alternating water levels (OBERDORFER 1993, p. 115). While species from flooded meadows occurred with medium frequencies, summer annual species from bur-marigold and orache bank communities were rare. Partly, this may be due to the weather conditions during fieldwork. Nonetheless, species from bur-marigold and orache bank communities seem to react more sensitively towards river regulation, as their habitat types are classified as strongly endangered according to the German Red List of endangered habitat types (FINCK ET AL. 2017). Thus, this habitat type is also protected by the Habitats Directive for Flora and Fauna (habitat type 3270: rivers with muddy with *Chenopodion rubri* p.p. and *Bidention* vegetation p.p.) (COUNCIL OF THE EUROPEAN COMMUNITIES 1992).

The decline of highly adapted species and the increase of less specialized species is a widespread phenomenon along regulated rivers (WALSH ET AL. 2005; HARVOLK ET AL. 2014), implying the high impact of regulation on an ecosystem that relies on disturbances by alternating water levels and flooding. The reduction in habitat dynamics and thus in habitat heterogeneity induces a shift in competitive structures in favour of competitive species (chapter 2), thus promoting homogeneity in species composition (WALSH ET AL. 2005). This aspect is also represented in the ordination diagrams in chapter 2 and chapter 3, as separation of vegetation relevés was less pronounced, although species abundances were transformed via square root transformation to represent rare species adequately. Nonetheless, the results of chapter 2, 3 and 4 also display that the hydrodynamic environment is still a major factor for habitat variability and species variability along highly regulated riverbanks. This finding is distinctly represented in the ordination diagram of chapter 3, where the environmental gradient reflecting bank steepness (Lahn: $r^2=0.069$ axis 1; Fulda: $r^2=0.172$ axis 2) explains less of the dataset variation than the environmental gradient for water level fluctuation (Lahn: $r^2= 0.225$ axis 1; Fulda: $r^2=0.234$ axis 2). As this aspect was also observed by XU ET AL. (2019) along the river Danube between Straubing and Vilshofen, restoration measures will contribute to a higher habitat heterogeneity along urban riverbanks.

1.4.2 Plant species diversity and functional diversity of riverbanks along Federal Waterways

Due to high habitat heterogeneity that is triggered by recurring flooding events, floodplain ecosystems exhibit an extraordinary high biodiversity (NAIMAN & DÉCAMPS 1997), wherefore these ecosystems are associated with a high ecological value. This applies to the large-scale assessment of floodplains but is not necessarily true for riparian areas in direct vicinity to water, as studied in this dissertation. These areas are defined by frequent water level fluctuations, which require special traits of plant species to cope with these conditions. Hence, an ecological assessment of riverbanks based on species diversity measures is strongly limited. This aspect is clearly represented in chapter 2: From plant species diversity perspective, riverbanks protected by ripraps were the most species-rich, by contrast to front-fixed and unfortified banks. Despite high levels of plant species diversity, species composition along ripraps mainly consisted of competitive species from terrestrial habitats, exhibiting a wide range of water demands. Compared to ripraps, front-fixed and unfortified banks were represented by lower species diversities, albeit they were characterized by a higher degree of habitat heterogeneity. Consequently, these bank types provide more niches for pioneer species with higher water demands, capable to cope better with alternating water levels than species from terrestrial habitats. Natural riverbank zones between mean and low-water line are less characterized by high species diversity levels than by high degrees of species adaptation (OBERDORFER 1993), which shows that the results related to species diversity (chapter 2) are congruent with literature. Moreover, as shown by PALMER ET AL. (2005), higher levels of riparian plant species diversity occur primarily as a consequence of the spread of competitive species due to reduced habitat dynamics. The results of comparative studies along regulated riverbanks display an ambivalent picture. While CAVAILLÉ ET AL. (2013) and BISWAS & MALLIK (2010) observed lower plant species diversity levels along intensively regulated riverbanks, HARVOLK ET AL. (2014) and NILSSON ET AL. (1994) detected higher levels in riparian plant species diversity.

Against this background, species diversity measures are suited as descriptive variables, but they are not appropriate for the qualitative assessment of the ecological state of riverbanks. As plant species traits are able to display the predominant ecosystem processes (BEJARANO ET AL. 2018b), functional diversity measures were calculated for data analysis in chapter 2 and 4 to enable an ecological assessment of riverbank habitats. According to TILMAN (2001), a high functional diversity in ecosystems is linked with a more efficient use of available resources compared to ecosystems with low trait diversity. Calculation of functional diversity measures was based on traits that were expected to vary due to water level fluctuations (PETCHEY & GASTON 2006). However, differences regarding functional divergence, functional dispersion (chapter 4) and Rao´s Q (chapter 2), whose calculation includes species abundances and which are suited to display trait differentiation (VILLÉGER ET AL. 2008; LALIBERTÉ & LEGENDRE 2010; RAO 1982), were marginal. Trait diversity and thus functional diversity of urban riverbanks is therefore considered as uniform, pointing to low abundances of highly adapted species. The generally weak grouping of relevés in the ordination diagrams of chapter 2, 3 and 4 also supports this finding, again pointing to low habitat heterogeneity along regulated riverbanks. This applies also to stretches along the river Lahn that are not classified as Federal Waterway and where regulation intensity (classified as weir-distant) is expected to be reduced due to the absence of locks in direct weir vicinity (chapter 4), which underlines the far-reaching consequences of river regulation measures for riverbank vegetation. However, it should be positively noted that at least the levels of functional richness of weir-distant sites were significantly higher compared to sites in the direct surrounding of weirs. In the calculation of this functional diversity measure, species abundances are omitted, wherefore functional richness reflects the trait diversity of a defined species community (VILLÉGER ET AL. 2008). This leads to the assumption of a higher presence of specialized species along riverbanks with lower regulation intensity and thus to a positive assessment of a significantly higher plant species diversity along these river stretches. Further, a higher functional evenness along weir-distant riverbanks indicates a higher use of resources (MASON ET AL. 2005) and thus a higher ecosystem functionality. These findings show that a lower regulation intensity provides potential for the enhancement of floristic diversity along banks of Federal Waterways. These findings also point out that the consideration of species traits are of essential meaning for the ecological assessment of riverbank vegetation along regulated rivers. Abundance-based methods and measures are no longer applicable to display differences in plant species composition of regulated riverbanks, as these are composed of species without special habitat requirements.

1.4.3 Measures for the floristic enhancement of Federal Waterways

Definition of the target state

An efficient investment of financial resources for river restoration measures requires the definition of a target state, also, to enable a subsequent measurement of success (PALMER ET AL. 2005). As emphasized in chapter 1.4.1, urban riverbanks nowadays are characterized by species from hardwood floodplains and terrestrial habitats that are mostly not typical for riverbank vegetation. As the potential natural vegetation of riverbank habitats consists of species from riparian habitats that are naturally free of woody vegetation and from species from the riparian softwood-land (ELLENBERG & LEUSCHNER 2010), restoration measures should be oriented towards the restoration of site conditions that favor these species. These species differ distinctly from terrestrial species in trait composition and may increase the functional diversity of floodplains and thus are suitable to enhance the floristic diversity along German Federal Waterways. This approach is in line with the findings of CAVAILLÉ ET AL. (2015) and GONZÁLEZ ET AL. (2017), who also use trait-based concepts for the definition of target states along regulated riverbanks.

Reduction of bank steepness

Typical riverbank plant species occurred along reaches with a higher frequency of water level fluctuations, wherefore restoration measures for urban riverbanks should consider this aspect. This can be achieved by the reduction of bank steepness and is further highly applicable to counteract the progressing terrestrialization in floodplains of highly regulated rivers (PEDERSEN ET AL. 2006). Along impounded Federal Waterways, this measure experiences a higher significance than along free-flowing rivers, as impounded rivers are affected by a higher reduction of flooding intensity, seasonality and frequency (JANSSON ET AL. 2000; POFF ET AL. 2007; POFF & ZIMMERMAN 2010) and population dynamics (ANDERSSON ET AL. 2000). Thus, measures to enhance the floristic diversity along impounded rivers are limited to the reduction of bank steepness. As shown by the field study along the rivers Main and Danube (chapter 1), a reduction of bank steepness to 10% is expected to show significant effects for the species composition of riverbank vegetation, since the plant species composition of front-fixed and unfortified banks was characterized by a higher proportion of typical riverbank species. As riverbanks protected by ripraps mostly exhibited a bank steepness of 24%, successful restoration measures for riverbanks consider a reduction of 60% in bank steepness to achieve a bank steepness of 10%.

Locality and type of impoundments

Single observations of summer annual *Bidentetea* species along flat banks (6% inclination) that were located downstream of weirs along the Lahn, higher frequencies of species from flooded meadows along the Fulda downstream reaches and generally more occurrences of species from habitats experiencing high disturbance levels (chapter 3) indicate the potential for the improvement of riverbank habitat quality by reduction of bank steepness. As downstream reaches exhibit a higher degree of hydrodynamics, also being more governed by seasonality than upstream reaches (upstream and downstream reaches are defined as reaches within a maximal distance of one kilometer to the weir), measures aiming at reducing bank steepness should mainly be carried out downstream of weirs. These measures provide not only the possibility for the promotion of typical riverbank species, but also to strengthen the already existing populations of species from flooded meadows and reeds of flowing waters, which are characteristic for riverbanks of free-flowing waters. Riverbank restoration measures located further downstream will also profit from these measures, as riverbank species composition is defined to a substantial part by upstream species occurrences (NAIMAN ET AL. 1993).

It has to be underlined that the discussed findings are only relevant for rivers that are impounded by weirs, which were mainly installed along waterways in the secondary Federal Waterways network. Water in rivers that are impounded by weirs runs permanently over the crest during the whole year, thus maintaining at least seasonal variations in mean water discharge along downstream river stretches (CSIKI & RHOADS 2010). Compared to the secondary Federal Waterways network, the flow regime in the primary Federal Waterways network is mainly determined by shipping traffic intensity. Therefore, the installed impoundments are not permanently overflowed by water, thus causing a higher decoupling of seasonal water level fluctuations. Consequently, downstream water level fluctuations in the primary Federal Waterways network are determined by shipping traffic intensity. They are of short duration, but occur more frequently compared to natural fluctuations, causing higher stress levels for riverbank vegetation (BEJARANO ET AL. 2018a). It is unlikely that the small and shallow-rooting *Bidentetea* species can resist those intensive water level fluctuations. In contrast to the downstream reaches in the secondary Federal Waterways network, downstream reaches in direct vicinity to impoundments in the primary Federal Waterways network are of minor importance for restoration measures. Against this background, riverbank restoration measures in the primary Federal Waterways network should be addressed outside of a distance of one kilometer upstream and downstream of impoundments.

Possibilities regarding bank structure

As discussed above, bank steepness, locality, and type of impoundment are essential factors to promote species that are adapted to fluctuating water levels along regulated riverbanks. As bank morphology contributes essentially to biodiversity in floodplains (PEDERSEN ET AL. 2006), this aspect plays also an important role in the development of a riverbank restoration concept for urban rivers (chapter 2). From species perspective, the Danubian unfortified riverbanks harbored the most typical species composition for riverbanks (FERSTL 2019), by contrast to the unfortified riverbanks along the river Main. The Danubian unfortified riverbanks had a concave character, were protected by ripraps at the concavities´ beginning and end and were secured by gravel in the transition zone, ensuring the reduction of wave intensity of inland waterway vessels. More typical riverbank plant species in the context of gravel additions in the transition zone were also observed by STROBL ET AL. (2015) along banks of the river Inn, which underlines the effectiveness of gravel additions in riverbank restoration planning. Similar to unfortified banks, front-fixed banks also showed a high effectiveness in the reduction of wave intensity. However, species composition was also characterized by species naturally occurring in near distance to oxbows, which are originally located in a higher distance to riverbanks. These species are typical for floodplains, but not typical for riverbanks, wherefore they are characterized as typical species in a broader sense. Therefore, this type of riverbank restoration measure is considered as subordinate compared to concave unfortified banks with gravel addition.

Unfortified and front-fixed banks are not only suited to promote a higher lateral connectivity between river and floodplain due to their low bank steepness. They also support higher sediment dynamics by cause of absent ripraps, wherefore these bank types are applicable to restore typical ecosystem functions (FLORSHEIM ET AL. 2008). Due to differences in riverbank species composition compared to ripraps and due to a stronger vertical layering, these bank types are also suitable to strengthen biotope-cross-linking along urban rivers (JONGMAN ET AL. 2004). A strong vertical layering reduces also the shading deficit along direct riverbank areas, therefore promoting higher variation in water temperatures, which is generally reduced in the riverbed of regulated rivers (BROOKS ET AL. 2006).

The growing implementation of front-fixed and unfortified banks along urban rivers will also have positive effects for population dynamics, which especially applies to reaches between impoundments. However, this is limited to the accessibility of source populations of target species, as these are of essential meaning for their colonization of target species along restored banks. Limiting riverbank restoration measures to the lowering of bank steepness without checking for accessibility of target population will not ensure the success of restoration measures. This aspect is pointed out in chapter 4: Although weir-near and weir-distant reaches shared similarities regarding the extent of water level fluctuations, the weir-near reaches exhibited a lower species variation due to a higher regulation intensity, albeit recurring disturbance events induce high variations in species composition (TOCKNER & STANFORD 2002). By contrast, riverbanks with low regulation intensity were characterized by higher variations in species composition and were enriched by typical species from habitats experiencing a higher frequency of water level fluctuations, contributing to a higher plant species and functional diversity. Thus, focusing solely on the restoration of water level fluctuations will not ensure success of riverbank restoration measures.

For reasons of traffic safety, it is very unlikely that riverbank protections along urban rivers will be removed. This relates in particular to areas directly downstream of impoundments, being highly stressed by fluctuating water levels, wherefore these areas are especially vulnerable to riverbank erosion. To counter riverbank erosion, ripraps were installed, though inducting profound alterations in the riverbank´s habitat quality (REID & CHURCH 2015). Nonetheless, it is possible to improve habitat quality, by decreasing bank steepness as much as possible in areas where flood protection measures remain unaffected and where the probability of riverbank erosion events is minimized. As shown by the results in chapter 1.4.1, at least typical riverbank species from flooded meadows occurred more frequently along banks with a maximum of 20% bank steepness. This would promote sedimentation processes and thus higher sediment dynamics in the hollows of ripraps, if the stone blocks are placed with sufficient distance between each other. By this, urban riverbanks could fulfill their original ecosystem services to a higher degree (FLORSHEIM ET AL. 2008). Higher sediment dynamics also provide ideal conditions for the establishment of woody structures, which fulfill important functions in prevention of riverbank erosion (HUBBLE ET AL. 2010) and regarding biotope-cross-linking along urban rivers (JONGMAN ET AL. 2004).

Compared to waterways in the primary Federal Waterways network, the use of secondary waterways is mainly limited to leisure purposes. This offers more possibilities for the ecological enhancement of riverbanks. Especially along the upstream reaches in a maximum distance of one kilometer to the next weir, the potential for riverbank erosion is expected to be the lowest, as water flow velocity is significantly reduced by the weir and riverbank erosion is consequently reduced to a minimum. Therefore, a first step to restore riverbanks along secondary waterways could be the removal of ripraps to promote sediment dynamics, thus enhancing a more natural riverbank protection by plant species of the nitrophilous tall herb communities (OBERDORFER 1993), which are widely spread along Federal Waterways.

1.5 Conclusions and perspectives for the assessment of successful restoration measures along Federal Waterways

The synthesized possibilities for riverbank restoration measures along urban rivers are developed based on site conditions along riverbanks in their unregulated state. Thus, restored riverbanks are not equal to unregulated riverbanks, as restored riverbanks still are determined by flooding events of less intensity, leading to narrower transition zones between aquatic and terrestrial habitats (BUNN & ARTHINGTON 2002). By contrast, transition zones of unregulated riverbanks are expected to be wider, as these sites naturally are subject to a higher frequency of water level fluctuations than habitats in more distance to the river, entailing higher sediment dynamics in direct vicinity to the river (ELLENBERG & LEUSCHNER 2010). As a consequence of a reduced longitudinal connectivity, regulated riverbanks are further characterized by lower population dynamics (ANDERSSON ET AL. 2000). Therefore, measures aiming at restoring riverine ecosystem functions ideally follow holistic approaches, considering the deficits in the adjacent catchment areas and the whole river as medium (PALMER ET AL. 2005). The restoration of longitudinal connectivity along intensively used water bodies like Federal Waterways is rather unlikely, wherefore the space for riverbank restoration measures is relatively small and limited to measures on local scale.

To at least promote habitat dynamics and habitat heterogeneity in selected areas, riverbank restoration measures should primary focus on the reduction of bank steepness to reduce the level of regulation intensity as far as possible. For reasons of infrastructure, the width of transition zones will not reach their natural state. Moreover, information on the state of origin is mostly not available, which impedes any planning of restoration measures. Further, it needs to be pointed out that the discussed measures were developed based on the actual state of riverbank plant species composition, wherefore they only apply to transition zone species that are still present along urban rivers. Consequently, it is not possible to evaluate to what extent disappeared plant species might profit. This point remains unanswered and needs to be addressed in an appropriate experimental setup. Against this background, the synthesized measures are suitable to reduce the regulation intensity along urban rivers, but they are not appropriate to restore the natural state.

River regulation measures date from the late 19^{th} century and further gained in intensity during the 20^{th} century (SCHIEMER ET AL. 1999; SHAFROTH ET AL. 2002). Due to this long time span, the affected ecosystems are disturbed by serious changes in structure and functionality, which is reflected by homogeneity in species composition and by the decline of highly specialized species. Therefore, it remains unanswered, whether the complete restoration of highly regulated rivers would lead to the complete restoration of riverbank plant species communities. Compared to free-flowing rivers, species composition of impounded rivers is affected to a higher degree by adjacent ecosystems that are also defined by anthropogenically induced changes (JANSSON ET AL. 2000), thus providing ideal site conditions for terrestrial and neophytic plant species (sensu KOWARIK). Especially neophytic plant species establish initial populations along sites that experienced human induced changes in habitat conditions (KOWARIK 2010, p. 112). This is displayed by frequent occurrences of neophytes along the middle Rhine valley riverbanks that experience high traffic intensities (KOSACK 2014), pointing to high niche availability in riverbank habitats. Thus, it remains unanswered, whether neophytes can replace traits of typical riverbank species.

Against this background, it is reasonable to assess changes in riverbank species composition by means of traits and not by means of species diversity measures. This also provides the opportunity to evaluate the success of restoration measures along urban rivers. The trait-based vegetation analyses in this dissertation showed that low competitive species with a short life span and high water demands from the summer annual *Bidentetea* plant communities generally occurred only fragmentary along transition zones of urban riverbanks (chapter 2, 3 and 4). Although weather conditions during summer 2018 were optimal for these species, they remained rare, which applies also to reaches with low regulation intensity (chapter 4). By contrast, species from flooded meadows that occur naturally above the *Bidentetea* species zone but still in the transition zone of riverbanks seem to react less sensitive towards river regulation, as they generally occurred more frequently than *Bidentetea* species. Species from flooded meadows are characterized by high regeneration capacity, high water demands and they are able to disperse both by seeds and vegetatively (OBERDORFER 1993). Occurrences of these species corresponded to the amplitude of water level fluctuations (chapter 2, 3 and 4), wherefore these species and their traits are suitable to indicate alterations in the hydrodynamic regime of regulated riverbanks more effective than *Bidentetea* species. This might also give orientation for the achievement of a good ecological potential along regulated rivers, which is defined as goal by the EU Water Framework Directive.

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Chapter 2

Dominance of competitors in riparian plant species composition along constructed banks of the German rivers Main and Danube

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Abstract

Hardening of shorelines has been extensively implemented in many parts of the developed world. This also applies to banks of German Federal Waterways, which are mostly fixed by ripraps to prevent bank erosion as a consequence of wave disturbance by shipping traffic. Since ripraps notably alter functions of riparian ecosystems and nature conservation demands recently gained in importance along waterways, alternatives for ripraps play an increasing role.

Front-fixed banks are ripraps parallel to the shoreline and embedded in the waterway´s channel with an unsecured bank of low steepness behind them. Thus, they are suitable to prevent banks from erosion. However, it is unclear how they can contribute to the ecological enhancement of riparian vegetation along waterways.

Therefore, we compared riparian vegetation of ripraps and front-fixed banks with unsecured banks along the German rivers Main and Danube to assess the ecological efficiency of front-fixed banks. Disturbance by alternating water levels was the lowest at ripraps, whereas disturbance levels were higher at front-fixed and unfortified banks. We used an ordination and indicator species analysis to reveal differences in species composition. The results of the indicator species analysis were analyzed regarding species´ biotope origin, light and moisture demand and life strategy. We analyzed species diversity and calculated functional diversity indices to display the prevalent ecosystem processes.

Higher variation in species composition, common indicator species, a strong vertical layering of woody riparian vegetation and similar site conditions at front-fixed and unfortified banks revealed higher similarities in species composition between them than to other bank type combinations. Limnic species occurred with a higher frequency at unfortified and front-fixed banks, whereas terrestrial species were more frequent at ripraps. Light-tolerant species were more common at ripraps, whereas species´ demand for moisture was higher at front-fixed and unfortified banks than at ripraps. Cr-strategists occurred more frequently with increasing disturbance level, whereas c-strategists were more common at ripraps.

Ripraps had the highest species diversity levels whereas functional diversity tended to be higher at front-fixed and unfortified banks. This indicates a higher trait complementarity and thus a higher specialization towards alternating water levels, wherefore a higher degree of naturalness can be assumed in these habitats.

Nature conservation efforts along German Federal Waterways should focus on the restoration of flooding dynamics, as species typical for riverine habitats are more common at front-fixed and unfortified banks than at ripraps. Since front-fixed banks bear traits suited for the reconnection of rivers and their floodplains and for bank protection, they are a suitable alternative to promote biodiversity along German Federal Waterways.

2.1 Introduction

Regulation measures like the installation of embankments along rivers led to fundamental changes in the natural flooding dynamic of running waters (LI AND EDDLEMAN, 2002) followed by a strong biodiversity loss in riparian habitats over time (DUDGEON ET AL., 2006; PAUL AND MEYER, 2001). In their original state, riparian habitats are characterized by recurring flooding events that create a high habitat heterogeneity (NAIMAN ET AL., 1993; WARD, 1998). As interfaces between aquatic and terrestrial zones, they provide highly diverse habitats for species adapted to recurring flooding events (NAIMAN AND DÉCAMPS, 1997) and serve as buffer between rivers and terrestrial ecosystems (PAUL AND MEYER, 2001). Due to their linear structure, birds and fishes use them as migration corridors (NAIMAN AND DÉCAMPS, 1997), which highlights their strong ecosystem network function abilities. Although riparian zones account for just 1.4% of the land surface area, at least 25% of all terrestrial ecosystem services are attributed to them (TOCKNER AND STANFORD, 2002).

Against the background of the high value of riverine habitats for biodiversity and landscape structure and the growing anthropogenic pressure, protection programs like the Convention on Wetlands (1971), the European Habitats Directive for Flora and Fauna (THE COUNCIL OF THE EUROPEAN COMMUNITIES, 1992) and the European Water Framework Directive (THE EUROPEAN PARLIAMENT, 2000) were approved. The European Water Framework Directive aims to achieve a good ecological status of all European rivers. Since a good ecological status concerns also morphological aspects like the structure of riparian zones along river bodies, a large number of restoration measures for the enhancement of their functionality were performed along German Federal Waterways during the last years (LORENZ ET AL., 2012).

Despite the increasing number of restoration measures, approximately 80% of the river banks along German Federal Waterways are still fixed by artificial bank protections like ripraps (L. SYMMANK, BfG, personal communication, September 25, 2017), mainly due to their cost-efficiency and simple installation (FISCHENICH, 2003). They are constructed to prevent bank erosion, which is caused by shear forces of waves initiated by shipping traffic (LI AND EDDLEMAN, 2002; REID AND CHURCH, 2015). Ripraps consist of loose and 40 to 80 cm thick stone fillings of varying size on top of a geotextile or a filter made of mineral grains from the bank bottom up to the bank edge with a bank steepness of 1:2 to 1:3 (L. SYMMANK, BfG, personal communication, October 1, 2018). Depending on their age, an overgrowth of herbs, shrubs and trees is possible, leading to various appearances. Nonetheless, the continuous installation of ripraps contributes to a uniform character of rivers with steep bank inclinations, which results in an interrupted lateral connectivity, a loss of flooding dynamics and a reduced sediment input (TOCKNER AND STANFORD, 2002; WARD, 1998). Due to their rocky structure, strong temperature fluctuations are expectable in summer

(CAVAILLÉ ET AL., 2013). Furthermore, their installation and maintenance require a removal of natural riparian vegetation, causing a reduced shading of the water body combined with a negative effect on aquatic organisms (LI AND EDDLEMAN, 2002). The space for riparian vegetation is restricted to a narrow belt characterized by severe alterations in habitat conditions (FISCHENICH, 2003) and plant species composition (HARVOLK ET AL., 2015).

In order to counteract these negative ecological impacts, the removal of ripraps became more and more relevant in recent years (L. SYMMANK, BfG, personal communication, November 30, 2017). However, riprap removal is challenging due to bank erosion risk along waterways with a high traffic volume. By contrast to ripraps, front-fixed banks are loose stone fillings (of varying height, width, and size of stones) parallel to the shoreline and embedded in the waterway channel with an unsecured bank of low steepness behind them. Thus, maintenance intensity at the river bank is reduced, which leads to a stronger vertical layering of woody vegetation. Compared to ripraps and front-fixed banks, along unsecured banks any form of a bank revetment is missing. Unfortified banks are characterized by an enhanced flooding dynamic due to a reduced bank steepness and maintenance intensity is comparable to front-fixed banks. By contrast, front-fixed banks show an improved suitability to prevent banks from erosion, while enabling a certain degree of flooding dynamics. Since front-fixed banks bear traits of ripraps and unsecured banks, this bank type might act as an ecologically suitable alternative for ripraps in the interplay between traffic safety and the improvement of the ecological situation along waterways. However, it is unclear how front-fixed banks can contribute to the ecological enhancement of riparian vegetation, as most studies to date focus on the ecological enhancement by bioengineering (BARITEAU ET AL., 2013; CAVAILLÉ ET AL., 2013).

To assess the ecological efficiency of front-fixed banks along waterways, we compared riparian plant species composition and diversity of front-fixed banks with riparian vegetation of ripraps and unfortified banks at eight study sites along the German rivers Main and Danube in Bavaria. As riparian vegetation of each river is specified by the river´s flow regime and geological understorey (NAIMAN ET AL., 1993; WARD, 1998), we investigated common trends along the Main and Danube to ensure transferability of our results to other rivers. Front-fixed and unsecured banks occur in Bavaria in a much higher local frequency than along other waterways in Germany, thus providing ideal study conditions. Furthermore, all study sites (four at each waterway) are characterized by damming for high shipping traffic, which offers comparable site conditions for our study.

The present study aims to evaluate differences regarding (1) species composition, (2) species´ ecological and functional traits and (3) species diversity and species functional diversity between ripraps, front-fixed and unfortified banks to display whether front-fixed banks can serve as an alternative for ripraps.

We hypothesize (a) that species composition and vegetation structure at front-fixed and unfortified banks show higher similarities due to greater comparability of site conditions and maintenance intensity. As flooding dynamics are anticipated to be higher along front-fixed and unfortified banks and species composition thus is predicted to be subject to stronger variation than along ripraps, the respective vegetation relevés are expected to take up more ordination space. Despite a higher variation in species composition, stronger similarities in species composition between front-fixed and unfortified banks should also be illustrated by common indicator species. Finally, similarities in vegetation structure are assumed to be displayed by higher coverages and heights of trees and shrubs.

Furthermore, we predict that (b) limnic species and species with improved adaptations to higher moisture levels occur more frequently than terrestrial species at front-fixed and unfortified banks. The csr-concept after GRIME (1979) describes species´ life strategy in response to disturbance events and resource availability and allows a species classification into functional groups. Thus, higher flooding dynamics at front-fixed and unfortified banks are also expected to be illustrated by a higher proportion of cr-strategists. By contrast, c-strategists are expected to occur more frequently at ripraps due to increased interspecific competition as disturbance frequency is assumed to be reduced. As a consequence of a stronger vertical layering of woody vegetation, more occurrences of less light demanding species are predicted at front-fixed and unfortified banks.

Finally, we expect (c) a lower species diversity due to increased flooding dynamics and thus improved species adaptation at front-fixed and unfortified banks. As improved adaptation to flooding dynamics is related to higher species´ trait differentiation, we assume higher levels of functional diversity.

2.2 Methods

2.2.1 Study areas

The study areas comprise stretches of the rivers Main (km 315 to 180; 198 m a.s.l (Obereisenheim) to 98 m a.s.l. (Marktheidenfeld)) and Danube (km 2348 to 2336; 313 m a.s.l.) in Bavaria, Germany (Fig. 2.1). Study sites of the Main are located in northwestern Bavaria in the area east and west of Würzburg (Obereisenheim, Kitzingen, Gemünden a. M., Marktheidenfeld). The study sites Marktheidenfeld, Kitzingen and Obereisenheim belong physiogeographically to the Franconian plates whereas Gemünden is part of the Spessart-Odenwald region (BAVARIAN STATE MINISTRY FOR REGIONAL DEVELOPMENT AND ENVIRONMENTAL ISSUES (StMLU), 1984). The alluvial soils in Obereisenheim and Kitzingen are characterized by Holocene drifting and terrace sands, whereas soils in Gemünden and Marktheidenfeld are formed by the older parent rocks of red sandstone. Dominating soil types are fluvisols and cambisols (BAVARIAN STATE OFFICE FOR ENVIRONMENT, 2017). The mean annual temperature is 9.6 °C and the mean annual precipitation is 601 mm (climate data for Würzburg from 1981 to 2010 (GERMAN METEOROLOGICAL SERVICE, 2017b)).

The Danubian study sites Pfatter, Irling, Aholfing and Obermotzing are located in southeastern Bavaria near Straubing. The study region belongs physiogeographically to the Bavarian tertiary molasse-hills, the Iller-Lech plates and the Danube valley (BAVARIAN STATE MINISTRY FOR REGIONAL DEVELOPMENT AND ENVIRONMENTAL ISSUES, 1984). The alluvial soils are formed by quarternary calcareous and sandy-loamy floodplain sediments transported by the Danube and its southern (Iller, Lech) and northern tributaries (Altmühl, Naab, Regen) resulting in calcareous fluvisols and cambisols as prevailing soil types (BAVARIAN STATE OFFICE FOR ENVIRONMENT, 2017). Compared to the Main valley, the climate along the Danube is characterized as cooler and wetter (Straubing: mean annual temperature: 8.6 °C; mean annual precipitation: 757 mm; climate data from 1981-2010 (GERMAN METEOROLOGICAL SERVICE, 2017a)).

The flow regime of both rivers is characterized as pluvial and determined by floods from December to April (KOENZEN, 2005) (Table 2.1 for detailed information regarding hydrology). The last extreme flooding event for both rivers was recorded in 2013, whereby the flooding impact was higher along the Danube (MERZ ET AL., 2014). Both waterways are connected via the Main-Danube Canal and categorized as waterways of international importance (Main: Va; Danube: VIb; FEDERAL MINISTRY FOR TRAFFIC AND DIGITAL INFRASTRUCTURE GERMANY, 2017) because of essential meaning for the transport of goods between the North and the Black Sea (MIHIC ET AL., 2011).

Table 2.1 - Hydrological parameters (mean ± standard deviation) of the Main and the Danube. Mean water discharge levels of the Main are displayed for Würzburg and refer to the period from 1989-2014 (BAVARIAN STATE OFFICE FOR ENVIRONMENT, 2013), whereas the Danubian mean water discharge levels refer to the measuring station of Bogen-Pfelling to the period from 1926-2012 (BAVARIAN STATE OFFICE FOR ENVIRONMENT, 2013). Data on water levels and their fluctuation as well as the number of flooding days were provided by the BfG. Site specific flooding durations were derived from 1D hydrological models implemented in FLYS 3.2.1 (GERMAN FEDERAL INSTITUTE OF HYDROLOGY, 2018). This software was developed by the German Federal Institute of Hydrology (BfG) and is based on long-term hydrological data (Main: 1965-2016; Danube: 1901-2008) and high-resolution digital ground models (Main: 2014; Danube: 2005). Asterisks mark the significance level (*p < 0.05; ** p < 0.01; *** p < 0.001) detected by ANOVA in R 3.2.2 (R DEVELOPMENT CORE TEAM, 2015). ANOVA aimed to detect statistical differences in the mean number of flooding days between bank types and was carried out for each river separately. Similar letters in the data on number of flooding days indicate homogenous groups according to a pairwise t-test including the Holm correction (p < 0.05).

		Main	**Danube**
Mean water discharge		127 m^3 s^{-1}	456 m^3 s^{-1}
Mean water level and fluctuation of the mean water level (2006-2015)		173.0 ± 45.1 cm	347.4 ± 44.6 cm
Mean water level and fluctuation of the mean water level (2016)		165.3 ± 26.3 cm	349.0 ± 37.9 cm
Mean number of flooding days (2016)*	Riprap	34.8 ± 26.4	4.3 ± 8.4 (a)
	Front-fixed banks	35.9 ± 31.7	19.6 ± 20.3 (ab)
	Unfortified banks	42.5 ± 30.3	26.9 ± 38.4 (b)

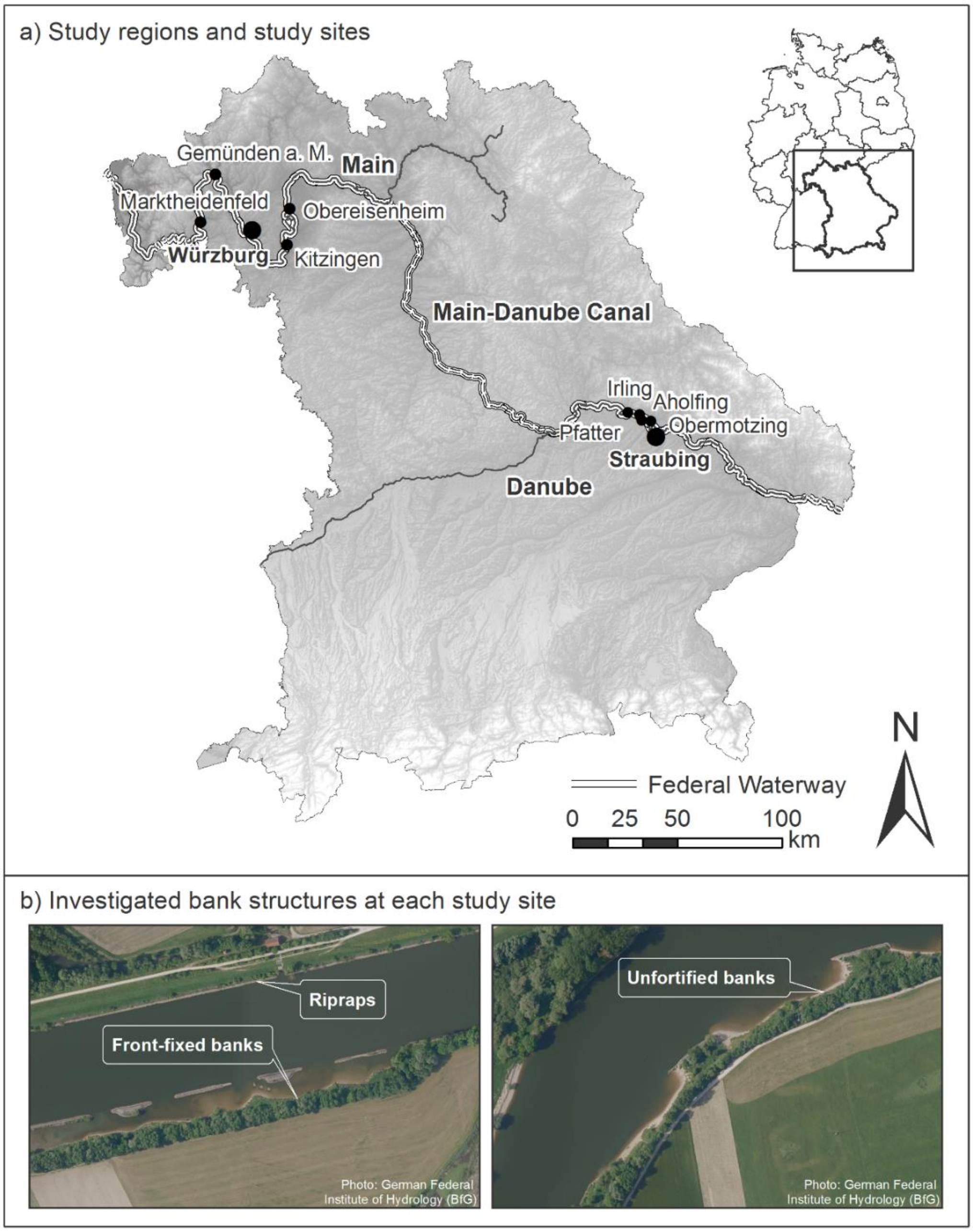

Fig. 2.1 - a) Location of the study regions (Würzburg, Straubing) and study sites (Main: Marktheidenfeld, Gemünden a. M., Kitzingen, Obereisenheim; Danube: Pfatter, Irling, Aholfing, Obermotzing) along the rivers Main and Danube with b) the aerial photographs of ripraps, front-fixed and unfortified banks by the example of Pfatter. Data sources for the data used for the map: Federal waterways, geographical data: German Federal Waterway Network, Version 1.1, provided by the BfG; digital elevation model: OpenDataBayern, provided by the Bavarian government; rivers: DIVA-GIS.

2.2.2 Study design, vegetation and environmental variables

Each study site covered a stretch of two kilometers distance, which contained river bank sections consisting of ripraps, front-fixed and unfortified banks (Fig. 2.1a and 2.1b, Table 2.2 for the description of structural characteristics and environmental conditions). As the impact of impoundments along waterways is expected to be the largest one kilometer upstream and downstream of the impoundment (J. SCHMIDT, Federal Waterways and Shipping Administration, personal communication, January 31, 2017), we ensured that all study sites were located outside of this area to exclude a direct impoundment effect (Table A2.12 for detailed information on dams). Within each study site, we randomly sampled four relevés for each bank type. Our sampling was strongly dependent of the spatial distribution of the studied bank types within each study site. Nevertheless, we made sure to keep a minimum distance of 30 to 50 m between the relevés. Due to limited accessibility in the field, we sampled three instead of four relevés along the front-fixed banks in Kitzingen and Aholfing. We recorded 12 relevés at each study site except for Kitzingen and Aholfing (11 relevés), resulting in 94 relevés in total. Each vegetation relevé was sampled in the riparian zone directly above the mean-water level in stretches of 10 m length along and 2 m width vertical to the river bank in early summer 2016 (May to July) (DYNESIUS ET AL., 2004). All samples were taken along the shoreline from the area regularly flooded. Vegetation samples at front-fixed banks were taken along the shoreline behind the riprap in the waterway´s channel. The estimation of species abundances was based on the modified Braun-Blanquet numerical scale (VAN DER MAAREL, 1979). Identification of plants followed the nomenclature of JÄGER (2013).

Sampling in the field included the documentation of coordinates, inclination, aspect, elevation, mean height (cm) and coverage (%) of each vegetation layer, litter and open soil (%). For detecting potential differences in the species composition of the studied bank types, the herb layer was subdivided into grass and herb fraction.

To gain information about the prevalent local site conditions, soil samples were taken from each vegetation relevé for further analyses. Soil sampling consisted of three soil cores randomly distributed across each vegetation sampling relevé with a *Puerckhauer*-boring rod (ø 2.5 cm) of the topsoil (0-10 cm) resulting in one mixed soil sample per relevé. Prior to further analyses, samples were dried and sieved (2 mm). The dominant soil type was determined by finger test (AD-HOC ARBEITSGRUPPE BODEN, 2005). Results of the finger test were very variable and revealed no patterns between bank types. Soil-acidity levels were measured by electrometer in H_2O and KCl (2,8 m) to get information about actual and potential acidity, respectively (PANSU AND GAUTHEYROU, 2006). The manometric technique according to Scheibler was used for the determination of soil lime content (MARTIN AND REEVE, 1955). Plant available phosphorus and potassium were determined by calcium-acetate-lactate (CAL) extraction (SCHÜLLER, 1969). Total carbon and nitrogen were detected by an elementary analyzer (Automatic Elemental Analyzer EA/NA 1110, TermoQuest Italia S.p.A.).

Table 2.2 - Structure and environment of the studied bank types. We estimated the ranges of the transitional zones between aquatic and terrestrial habitats for each bank type in the field. Data on bank inclination, vegetation structure, abiotic and biotic parameters (mean ± standard deviation) were calculated from the observed data for each relevé. Asterisks mark the significance level (*p < 0.05; ** p < 0.01; *** p < 0.001) detected by a Kruskal-Wallis test in Statistica 13. Similar letters indicate homogenous groups according to Mann-Whitney-U-Test (p < 0.05). Data on vegetation structure and abiotic parameters refer only to relevés in which the parameters were observed. Photographs of the riprap and unfortified bank are taken from the river Danube and photograph of the front-fixed bank from the river Main.

Bank revetment		**Riprap (n=32)**	**Front-fixed bank (n=30)**	**Unfortified bank (n=32)**
				
Transition zone	Range	Narrow, less than 1 m	Wider, up to 2 m	Wider, up to 3 m
Bank structure	Embankment design	Riprap	Riprap parallel to the shoreline embedded in the waterway channel, unfortified bank structure	Absence of riprap, unfortified bank structure
	Bank inclination (%)***	23.1 ± 10.7 a	9.5 ± 7.4 b	8.3 ± 4.6 b
Flooding	Flooding dynamics	Low	High	High
	Flow velocity	Depending on stream velocity	Calmed flow to stagnant water body	Calmed flow
Abiotic parameters	Relevés with open soil	3	6	17
	Coverage open soil (%)	16.7 ± 7.6	13.3 ± 4.1	22.1 ± 10.5
Vegetation structure	Tree layer (n relevés)	11	17	14
	Coverage (%)*	33.6 ± 17.3 a	59.7 ± 25.8 b	45.4 ± 29.9 ab
	Height (m)**	9.5 ± 4.5 a	15.9 ± 2.2 b	14.3 ± 4.8 b
	Shrub layer (n relevés)	22	19	17
	Coverage (%)	26.4 ± 17.1	28.8 ± 14.5	28.8 ± 19.3
	Height (m)	3.2 ± 2.0	3.1 ± 2.2	3.9 ± 2.9
Biotic parameters	Litter (n relevés)	12	18	10
	Coverage (%)***	9.6 ± 1.4 a	23.6 ± 11.4 b	15.0 ± 7.1 ab

2.2.3 Statistical analyses

Non-metric multidimensional scaling (NMS) was used to display similarities and dissimilarities in species composition between the bank types and the most important environmental gradients that determine the variation in species composition. Distances are represented by the Sørensen distance measure (Bray-Curtis distance) and 200 iterations; three dimensions and a random starting configuration were adjusted for the performance of the analyses. Prior to the ordination, abundance data were transferred into percentage values and transformed via square root transformation for an improved representation of rare species. NMS was performed with PC-ORD 7 (MCCUNE AND MEFFORD, 2006). A first ordination of the vegetation data revealed major differences in species composition between both rivers. Since our study aims to detect differences in species composition between the described bank types, all subsequent analyses were executed separately for each river and common trends were considered.

For the determination of significant indicator species for each bank type, an indicator species analysis (ISA) was performed (DUFRÊNE AND LEGENDRE, 1997). The advancement of CÁCERES ET AL. (2010) allows the detection of indicator species for combinations of study sites. With respect to potential similarities in species composition between the studied bank types, this tool is of high suitability. Significant indicator species have an indicator value (IV) > 25 and a p-value < 0.05 (DUFRÊNE AND LEGENDRE, 1997). ISA was performed with the R-package *indicspecies* (CÁCERES ET AL., 2009) in R 3.2.2 (R DEVELOPMENT CORE TEAM, 2015).

Species diversity was analyzed using the diversity indices Richness, Shannon index (SHANNON AND WEAVER, 1963) and Evenness (HILL, 1973). Calculation of diversity measures was executed using Turboveg 2.127 (HENNEKENS AND SCHAMINÉE, 2001).

By contrast to species diversity measures, functional diversity measures are able to display the degree of niche differentiation and thus species´ adaptation to different hydrodynamic conditions (BEJARANO ET AL., 2018). Thus, these measures are appropriate to display the predominant environmental processes (BEJARANO ET AL., 2018; GONZÁLEZ ET AL., 2015; MOUILLOT ET AL., 2013). We used this approach to assess the ecological effectiveness of front-fixed and unfortified banks along waterways. Analysis of functional diversity was carried out with five functional diversity indices: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) (VILLÉGER ET AL., 2008), functional dispersion (FDis) (LALIBERTÉ AND LEGENDRE, 2010) and Rao´s quadratic entropy (RaoQ) (RAO, 1982). Each measure is applicable to represent a different aspect of functional diversity to obtain an entire picture of the prevalent functional trait space (LALIBERTÉ AND LEGENDRE, 2010; MASON ET AL., 2005). Selection of appropriate traits for the calculation of functional diversity needs to take the specific context of interest into account (PETCHEY AND GASTON, 2006). Since flooding and disturbance events are among the main driving factors in riparian habitats, we selected functional traits that are likely to be affected by this factor: Guild, maximum height, life span, position of the regeneration organs, ecological optimum for moisture as well as tolerance for periodic wetness and flooding (Table A2.1 (MERRITT ET AL., 2010)). The Ellenberg indicator values (EIV; ELLENBERG ET AL., 1991) and the databases BIOLFLOR (KÜHN ET AL., 2004) and LEDA (KLEYER ET AL., 2008) served as data sources for ecological and trait values. Calculation of functional diversity measures was executed with the R-package *FD* (LALIBERTÉ AND LEGENDRE, 2010) in R 3.2.2 (R DEVELOPMENT CORE TEAM, 2015).

Statistical differences regarding the number of flooding days at each bank type (Table 2.1) were validated by means of ANOVA ($p<0.05$) and a subsequent pairwise t-test including the Holm correction to determine homogenous groups in R 3.2.2. We used a Kruskal-Wallis test by ranks in Statistica 13 (STATSOFT, 2017, Tulsa, OK, USA) for reasons of inhomogenous variances and for lack of normally distributed data to test for statistical differences in species diversity and functional diversity as well as vegetation structure (Table 2.2) and soil chemical analyses (Table A2.4) among the studied bank types. Homogenous groups were identified with the Mann-Whitney-U-Test ($p < 0.05$).

2.2.4 Analysis of ecological and functional groups

Since an ISA detects not only significant indicator species, but also groups of species that tend to occur mainly at one site but are not significant indicator species, the resulting species lists were used for further analyses focusing on species´ ecological and functional traits.

We analyzed species´ habitat preferences with their binding to either terrestrial or limnic habitats. To gain detailed information regarding species´ adaptations to moisture and light conditions, we used species´ Ellenberg indicator values (EIV) (ELLENBERG ET AL., 1991) for moisture and light. Adaptation to higher moisture levels is reflected by a higher EIV for moisture (>6), whereas light demanding species are characterized by a higher EIV for light (>5). To display species´ life strategy in response to disturbances by water level fluctutation, we used the csr-concept after GRIME (1979).

Data describing the habitat preference and the life strategy type were extracted from the BIOLFLOR database (KÜHN ET AL., 2004), indicator values for moisture and light from the EIV (ELLENBERG ET AL., 1991).

2.3 Results

2.3.1 Species composition

In total, we recorded 161 species along the Main and 136 species along the Danube resulting in 223 species for the combined dataset and 75 species (33.6%) common for both. In 47 vegetation surveys of the Main, *Urtica dioica* (38x), *Calystegia sepium* (33x), *Phalaris arundinacea* (33x) and *Chaerophyllum aureum* (27x) were the most frequent species. *Festuca arundinacea* (43x), *Poa palustris* (40x), *Rubus caesius* (33x) and *Urtica dioica* (33x) were most common along the Danubian river banks. All species are characteristic for the nitrophilous tall herb communities of river banks – except for *Festuca arundinacea*, which is a common species for flooded meadows. Across all study sites, *Galium verum* occurred only at the ripraps and *Trifolium pratense* was restricted to the front-fixed banks. The unfortified banks had no species in common.

NMS for the relevés of both rivers revealed a clear arrangement according to their geographical distribution (Fig. 2.2a). More ordination space and a grouping of the relevés from front-fixed and unfortified banks to ripraps was apparent in both datasets. The Main relevés covered a larger ordination space than those from the Danube. Relevés from the Danube were characterized by an origin of higher elevation and higher lime content in water and soil, whereas soils at the Main showed higher phosphorus contents. A grouping of relevés according to bank type was more apparent at the Danubian relevés. Generally, ripraps tended to show a higher species diversity, whereas the vector indicating the number of flooding days for each bank type and the vector of EIV for moisture tended to be associated to front-fixed and unfortified banks along the Main (also apparent in Fig. 2.2b).

With a view to the ordination plot of separate NMS for the Danube dataset (Fig. 2.2c), the patterns of a higher number of flooding days and thus moister site conditions (vector EIV Moisture) at front-fixed and unfortified banks can be also confirmed for relevés sampled along the Danube. NMS for the Main revealed an inverse relationship between a higher bank inclination at ripraps and an increasing number of flooding days (Fig. 2.2b). Furthermore, separate NMS for both waterways implied the tendency of a stronger vertical layering of woody vegetation at front-fixed and unfortified banks, whereas species occurring in ripraps tended to show adaptations to lighter site conditions, revealed by a longer vector EIV for light at least at the Main. These patterns can also be observed for the Danubian data, as indicated by the vector for the coverage of trees and shrubs (Fig. 2.2c). Coverage of grass increased at sites with weaker vegetation structure at both rivers. Our results are well underlined by Table 2.2, which contains detailed information about the characteristics of the transition zone, the structure of each bank type and the resulting flooding dynamics, the vegetation structure and abiotic and biotic parameters.

ISA detected more significant indicator species for the Main than for the Danube (Table 2.3). The highest numbers of significant indicator species with various adaptations to moisture were found at ripraps (Table 2.3). Two species were identified as common indicator species for the front-fixed and the unfortified banks (*Humulus lupulus, Iris pseudacorus*).

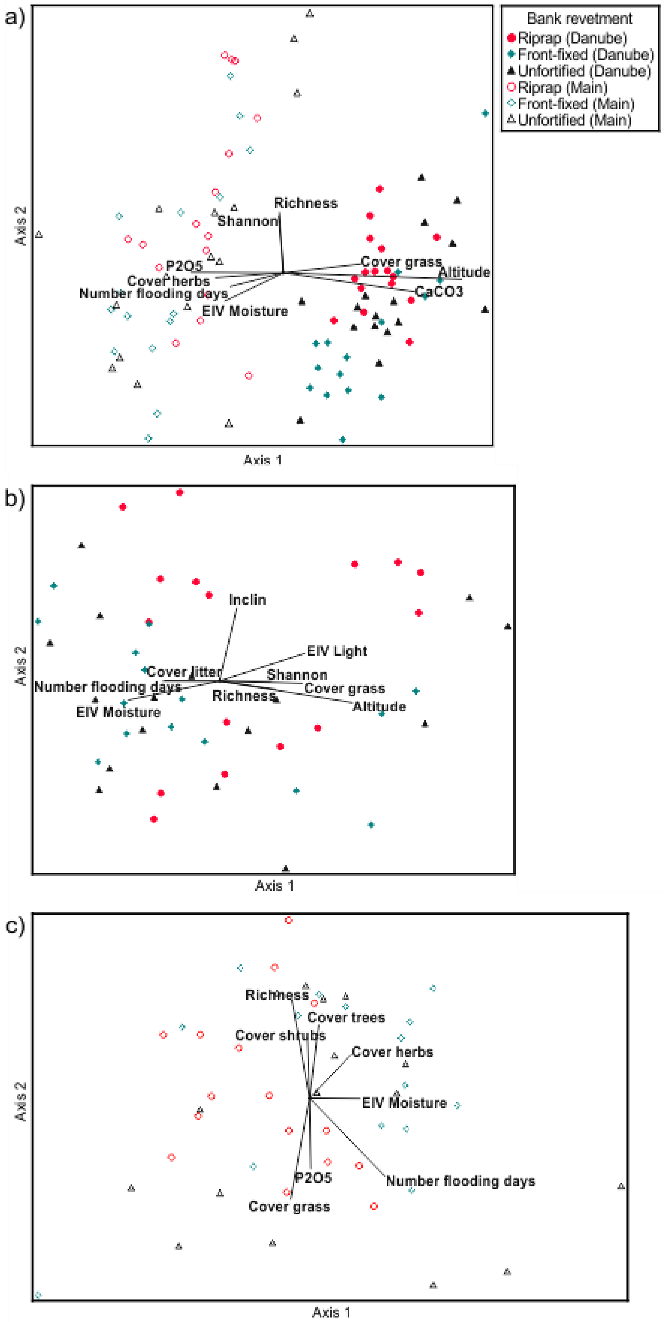

Fig. 2.2 - Final three-dimensional NMS for Main and Danube River vegetation data. Every point displays one vegetation survey. Figure a) displays the NMS plot of the whole dataset with a final stress of 16.31. All environmental variables with $r^2 > 0.2$ are shown. 77.2% of the variance in the dataset is explained by axis 1 (r^2=0.359), axis 2 (r^2=0.262) and axis 3 (r^2=0.150; not shown). Figure b) displays the NMS plot of the Main-River with a final stress of 15.58. All environmental variables with $r^2 > 0.2$ are shown. 76.2% of the total variance in the dataset is explained by axis 1 (r^2=0.458), axis 3 (r^2=0.178) and axis 2 (r^2=0.127; not shown). Figure c) displays the NMS plot of the Danube-River with a final stress of 15.45. All environmental variables with $r^2 > 0.15$ are shown. 80.3% of the variance in the dataset is explained by axis 1 (r^2=0.455), axis 2 (r^2=0.218) and axis 3 (r^2=0.130; not shown). See Table A2.2 for the description of the environmental variables.

Table 2.3 - Results of the indicator species analysis for the bank types (riprap (R; n=16), front-fixed (F; n=15), unfortified (U; n=16)) and the combinations of bank types for each waterway. Indicator species are characterized by an indicator value (IV) >25, a p-value <0.05 (Monte Carlo randomization test) and an Ellenberg indicator value (EIV) for moisture. Species with high EIV are more moisture-adapted than species with low EIV (ELLENBERG ET AL., 1991). Species with an "x" show no reactions to changes in moisture conditions.

	Waterway	**Main**				**Danube**			
	Bank type	**Indicator species**	**IV**	**p-value**	**EIV moisture**	**Indicator species**	**IV**	**p-value**	**EIV moisture**
Bank type	R	*Salix purpurea*	75.3	0.001	x	*Angelica archangelica*	64.7	0.001	9
		Geranium pratense	68.1	0.005	5	*Solanum dulcamara*	62.2	0.003	8
		Barbarea vulgaris	53.9	0.007	6				
		Iris pseudacorus	53.5	0.016	9				
		Lamium album	52.1	0.017	5				
		Scrophularia auriculata	53.2	0.018	9				
		Acer pseudoplatanus	50.0	0.028	6				
		Ranunculus acris	47.8	0.048	x				
	F	*Salix eleagnos*	44.7	0.027	7	*Deschampsia cespitosa*	51.6	0.007	7
		Epilobium parviflorum	44.7	0.029	9				
		Salix fragilis	43.8	0.046	8				
	U	-				*Silene vulgaris*	49.1	0.033	4
Combinations	R + F	-				-			
	R + U	-				*Galium album*	84.6	0.001	x
						Arrhenatherum elatius	83.0	0.001	x
	F + U	*Humulus lupulus*	62.1	0.045	8	*Iris pseudacorus*	57.8	0.032	9

2.3.2 Species´ ecological and functional traits

Limnic biotope species occurred more frequently at unfortified banks and with the lowest frequency at ripraps (Fig. 2.3a), whereas a consistent species pattern for front-fixed banks was not detectable. Vice versa, species of terrestrial biotopes showed the highest frequencies at the Danubian ripraps (Fig. 2.3b), whereas front-fixed and unfortified banks showed decreasing trends. Additionally, terrestrial biotope species occurred more often at the Danube than at the Main, where the proportion of terrestrial biotope species was slightly higher at ripraps. At both waterways, light demanding species grew more often at ripraps characterized by weaker vertical layering of the vegetation (Fig. 2.3c). By contrast, species occurring at front-fixed and unfortified banks tended to show better adaptations towards light deficiency (Fig. 2.3c) and to high water supply (Fig. 2.3d).

Species associated to unfortified banks are mostly identified as cr-strategists (Fig. 2.3f), whereas c-strategists occurred in a higher frequency at ripraps (Fig. 2.3e). At the front-fixed banks, no clear pattern was visible. Apart from a small number at the Main River ripraps, s-strategists were absent (Table A2.11). By contrast, r-strategists occurred a little more frequently but were still seldom in the whole dataset (Table A2.11). A bank-dependent pattern was not observable.

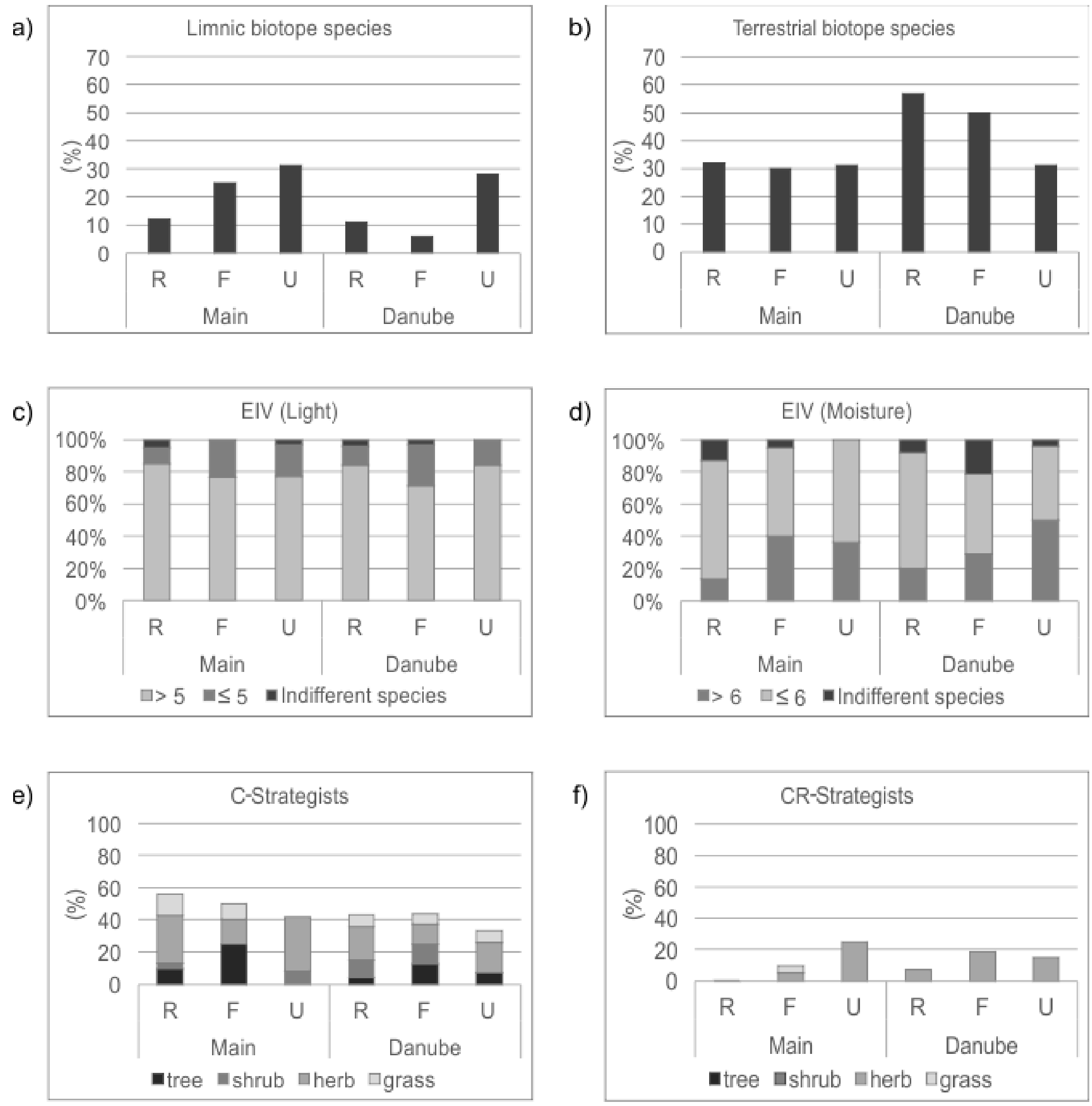

Fig. 2.3 - Results of the ecological and functional trait analysis of groups of site-associated species detected by ISA for each waterway and bank type (riprap (R), front-fixed (F), unfortified (U)). Figure a): Species with an EIV>5 have higher light requirements than species with an EIV≤5. Figure b): Species with an EIV>6 tend to be more moisture-adapted than species with an EIV≤6 (ELLENBERG ET AL., 1991). Indifferent species do not react to the indicated environmental factor. Figure c) and d) refer to species with a complete habitat binding to either limnic or terrestrial biotopes (Data from BiolFlor (KÜHN ET AL., 2004)). Figure e) and f) refer to species that are either c-strategists (competitor (C)) or cr-strategists (competitor and ruderal (CR)) (GRIME, 1979).

2.3.3 Diversity and functional diversity

Diversity levels at the Main tended to be higher than at the Danube. The highest diversity levels were observed at ripraps (Fig. 2.4), with significant differences to front-fixed banks for Shannon-Diversity and Evenness at the Main and Shannon-Diversity and Richness at the Danube. Unfortified banks mostly tended to show slightly higher diversity levels than front-fixed banks.

Except for levels of FEve at unfortified banks at the Danube, analysis of functional diversity revealed mostly non-significant results. Trends for FRic (Fig. 2.5 and f), FDis (Fig. 2.5d and i) and RaoQ (Fig. 2.5e and k) are consistent for all bank types at both waterways. Higher levels of FRic display the broader species spectrum at ripraps. Front-fixed banks bear the species composition with the highest trait differentiation, which is indicated by FDis and RaoQ. The lowest species´ trait differentiation was calculated for ripraps.

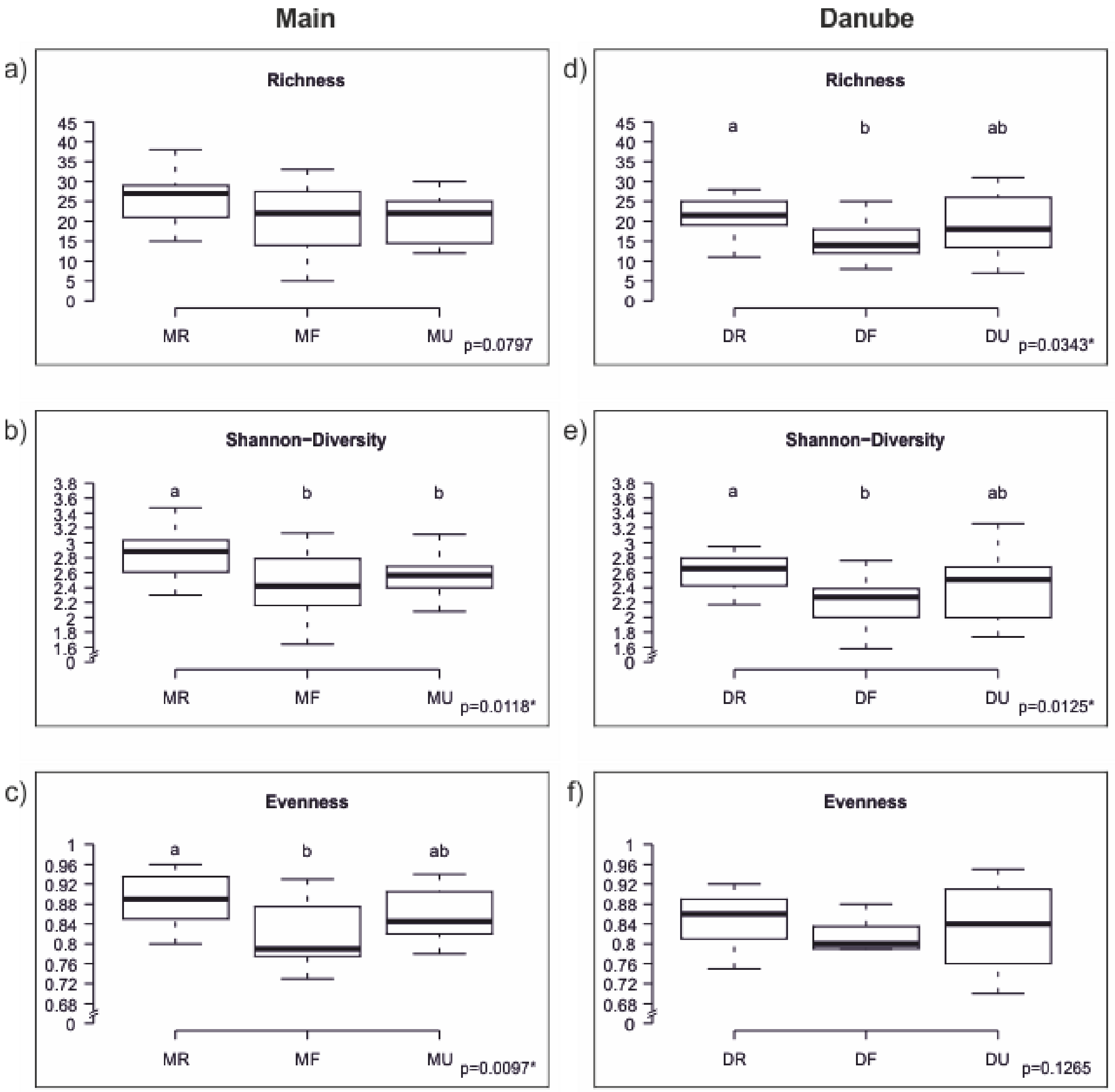

Fig. 2.4 - Results of the Kruskal-Wallis test by ranks (significance level: $p<0.05$) for species diversity measures for each waterway (Main (M), Danube (D)) and bank type (riprap (R; n=16), front-fixed (F; n=15), unfortified (U; n=16)). For reasons of readability Y-axes do not start at zero and show a broken line.

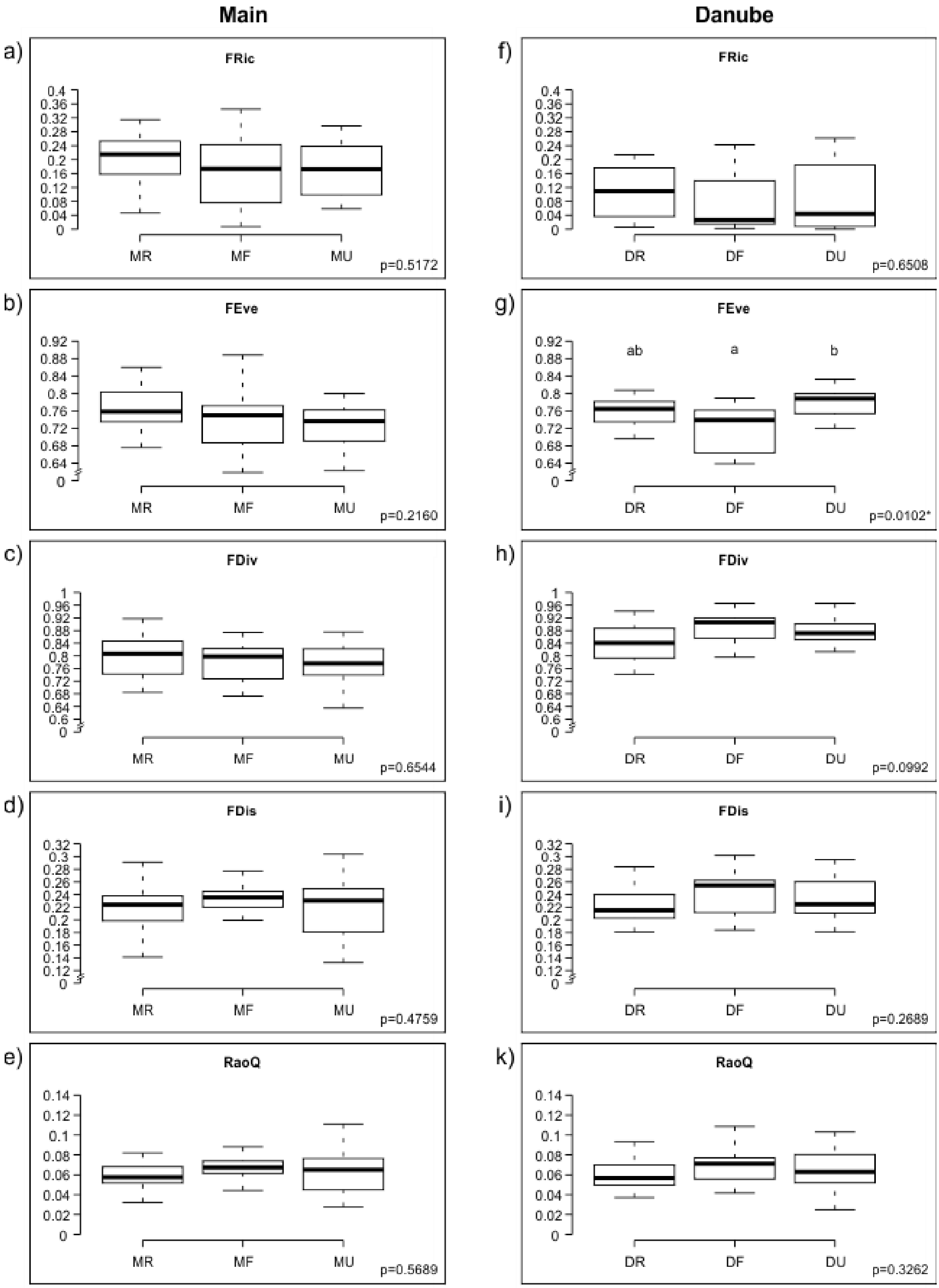

Fig. 2.5 - Results of the Kruskal-Wallis test by ranks (significance level: $p<0.05$) for functional diversity measures functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dispersion (FDis) and Rao´s quadratic entropy (RaoQ) for each waterway (Main (M), Danube (D)) and bank type (riprap (R; n=16), front-fixed (F; n=15), unfortified (U; n=16)). For reasons of readability Y-axes do not start at zero and show a broken line.

2.4 Discussion

2.4.1 Species composition of front-fixed and unfortified banks shows contrasts to ripraps

Despite clear regional differences in species composition, species composition at front-fixed and unfortified banks show contrasts to ripraps, as NMS revealed a grouping of the relevés from front-fixed and unfortified banks to ripraps and ISA showed common indicator species. The regional differences can be explained by differences in the geological understorey. The Danubian soil samples were characterized by a higher lime content than those along the Main, as the Danubian catchment is fed by inflows from the Franconian and the Swabian Jura and the Northern Limestone Alps (BAVARIAN STATE OFFICE FOR ENVIRONMENT, 2018). This displays the high relevance of the geological understorey, with seasonal fluctuations of magnitude, frequencies and duration of flows majorly determining riverine species composition (MERRITT ET AL., 2010). A closer inspection of the hydrological parameters (Table 2.1) shows that both rivers reveal similar long-term levels of water level fluctuation (2006-2015). This underlines the high regulation degree of the Main and the Danube, thus reducing the meaning of hydrological variations for riverine species composition along waterways and underlining the importance of our study for approaches on the promotion of typical riparian species along waterways.

The high regulation degree might also be the reason for the delicate grouping of the relevés according to the bank type within relevés of the Main and the Danube. Nevertheless, a grouping of the relevés from front-fixed and unfortified banks to ripraps was apparent along both rivers. Species composition of the front-fixed and unfortified banks showed higher variation than ripraps. This is reflected by a larger ordination space covered by the relevés of the front-fixed and unfortified banks (particularly recognizable in Fig. 2.2a) and evidently less significant indicator species at front-fixed and unfortified banks along both waterways (Table 2.3). We explain this aspect by a higher influence of disturbance by flooding, which is represented by the vector for the number of flooding days in all ordination plots. Furthermore, Table 2.1 reveals a higher number of flooding days at front-fixed and unfortified banks especially at the Danube, which might also be a reason for the clearer grouping of the respective relevés in the NMS plot. The inverse relationship between the vector of bank steepness and the number of flooding days in Fig. 2.2b (Inclin) shows well that front-fixed and unfortified banks are less steep than ripraps, resulting in a wider area that is influenced by a higher level of flooding disturbance. This factor is known to be a key component in structuring riparian vegetation (MERRITT ET AL., 2010). Higher variations in species composition of stretches exposed to alternating water levels were also found in HARVOLK ET AL. (2014) and PEDERSEN ET AL. (2006).

Generally, NMS revealed higher variation for the Main than for the Danube dataset. We explain this aspect by differences related to the distance between study sites, which were larger along the Main. Thus, variation in species composition was higher, making it difficult to prove a bank type related effect at the Main in the NMS. Moreover, it is important to mention that relevés of one study site were sampled within a stretch of two kilometers, also accounting for some similarities in species composition between relevés within one study site and being an explanation for a delicate grouping in the NMS plots. Nevertheless, we used this method to display common similarities and dissimilarities in species composition and the most conclusive environmental factors for the variation in species composition.

Since ISA revealed common indicator species for front-fixed and unfortified banks along both rivers (Main: *Humulus lupulus*, Danube: *Iris pseudacorus*), we assume higher similarities in species composition for front-fixed and unfortified banks. *Humulus lupulus* and *Iris pseudacorus* are typical species in the softwood floodplain (OBERDORFER, 1992, 1993) which show a high demand for moisture (ELLENBERG ET AL., 1991), thus well reflecting higher flooding dynamics as a consequence of the reduced bank steepness at front-fixed and unfortified banks.

Front-fixed and unfortified banks show also similarities regarding the prevalent vegetation structure (Table 2.2, Fig. 2.2), which was characterized by a strong vertical layering of woody riparian vegetation, thus leading to more occurrences of more shadow-tolerant species (Fig. 2.3c). This points to a higher habitat heterogeneity, which plays an important role for niche differentiation and thus high biodiversity in natural floodplains (SCHIEMER ET AL., 1999; TOCKNER AND STANFORD, 2002). Similar findings were made by GURNELL ET AL. (2007), who recognized a negative relationship between embankments, habitat complexity and floodplain connectivity due to higher maintenance intensity. A higher amount of trees along waterways provides effective barriers for sediment retention (GURNELL AND PETTS, 2006), bank stabilization (HUBBLE ET AL., 2010), regulation of light and temperature in the streambed and food sources for aquatic organisms (NAIMAN ET AL., 1993). Hence, front-fixed and unfortified banks promote biotope cross-linking along waterways (JONGMAN ET AL., 2004) and contribute to a higher habitat heterogeneity.

Due to common indicator species and similarities regarding composition and structure, our results demonstrate that front-fixed and unfortified banks bare similar site conditions between each other and show contrasts to ripraps. As front-fixed banks enable on the one hand higher dynamic by alternating water levels and on the other hand biotope cross-linking and a higher habitat heterogeneity along waterways, they are of higher nature conservation value than ripraps. Against this background, they are a good alternative for the prevention of bank erosion along waterways.

2.4.2 Species' ecological and functional traits of front-fixed and unfortified banks differ to ripraps

Species occurring at front-fixed and unfortified banks are under more influence of disturbance by flooding, which is displayed by a higher number of flooding days at these sites (Table 2.1, Fig. 2.2). Therefore, they are related to moister site conditions, which becomes clear through the spreading of the respective relevés mainly near the vector of EIV for moisture in the NMS plots (Fig. 2.2 but also Table 2.3 and Fig. 2.3d). By contrast, indicator species of the ripraps at the Main showed a larger variation of the EIV for moisture than indicator species of the front-fixed banks. It indicates that the prevalent site conditions are less influenced by high water levels. Thus, habitat is also available for species with lower demand for soil moisture levels like *Geranium pratense* (EIV 5) or for species that react indifferently to moisture like *Ranunculus acris*. This is due to the high bank steepness, leading to a considerably narrower transition zone between water and land, which is characteristic for channelized streams (PEDERSEN ET AL., 2006). The resulting strong moisture gradient leads to a shift in species composition (HARVOLK ET AL., 2014), promoting species from upland habitats like *Agrostis stolonifera* or *Sedum acre* with more moderate moisture preferences, also known as terrestrialization (CATFORD ET AL., 2014; DÉCAMPS, 2011). This is underlined by our findings of the species´ origin. Terrestrial biotope species occur with a higher frequency at ripraps, whereas limnic biotope species such as *Rorippa amphibia* and *Veronica maritima* are found more often at front-fixed and unfortified banks. This implies that restoration measures aiming to restore a higher degree of flooding dynamics are suited to promote characteristic riparian vegetation and to counteract terrestrialization along waterways. Our findings are well in line with the results of similar studies (CLARKE AND WHARTON, 2000; HARVOLK ET AL., 2014; HARVOLK ET AL., 2015; PEDERSEN ET AL., 2006). The main reasons for the terrestrialization process along waterways are hydrological alterations of the flooding regime (CATFORD ET AL., 2014), leading to a decoupling between rivers and floodplains (DÉCAMPS, 2011) as a consequence of the installation of embankments like ripraps (DEILLER ET AL., 2001) and the deepening of the streambed. Since riparian vegetation of the Danube showed a higher proportion of terrestrial species, the process of terrestrialization might be more pronounced than at the Main. A relatively stronger deepening of the Danubian streambed possibly leads to a notable groundwater table dropdown (WARD, 1998). Although the Danube experiences flooding events during springtime, which are related to a certain degree to alpine snowmelt (GLASER ET AL., 2010), these flooding events might not be suitable to weaken the long-term effect of streambed deepening (BEJARANO ET AL., 2018), thus illustrating the extent of hydrological alterations along waterways.

Differences in site conditions also become apparent with regard to the survival strategies of the observed plants, which are known to be determined by disturbance events and resource availability (GRIME, 1979). According to GRIME (1979), c-strategists mainly occur in productive environments without disturbances, competing with other species for all available resources. In contrast to that, species with a ruderal strategy are characterized by fast growth, high seed production and a short life span and can be found at potentially productive sites with frequent disturbances. These species frequently occur at temporary open muddy or gravel banks, with high water and nutrient supply (OBERDORFER, 1993), being representative for rivers with a flooding regime not affected by regulation measures. Due to the harmonization of riverbeds for undisturbed shipping traffic along rivers, these sites became seldom in recent years, thus explaining the rareness of these species in our dataset and underlining the ecological extent of these alterations. Species composition of ripraps was mostly dominated by c-strategists like *Festuca rubra* and *Galium album*, whereas an increasing proportion of species of unfortified banks were cr-strategists. This points to a more frequent occurrence of pioneers at these sites, again implying that these sites promote characteristic riparian species. Bank morphology is proved to be a key driver of species composition in riparian areas (PEDERSEN ET AL., 2006). A higher proportion of pioneers due to more disturbance was also found by CAVAILLÉ ET AL. (2015), GONZÁLEZ ET AL. (2017) and BAART ET AL. (2013). At unfortified banks a higher proportion of cr-strategists is expectable, as wave exposure is higher, thus reflecting different disturbance levels than at ripraps. Clear patterns for species strategies at front-fixed banks remained elusive, possibly for reasons of a lower disturbance by waves due to the front-fixed riprap, which is more distinct at the unfortified banks. WEBER ET AL. (2012) studied the effect of front-fixed banks along the Havel River and found a significant decrease of wave impact at these sites, resulting in higher abundances and diversity of macrophytes. They stated furthermore that reduced wave dynamic promotes the development of reed stands, which is the typical vegetation of oxbows. Oxbows used to be a typical element of unaltered floodplain systems but were largely removed during regulation measures.

Our results display the ecological consequences of river regulation for plant species along waterways. R-strategists were rare, cr-strategists occurred mainly along unfortified banks and species at front-fixed banks showed better adaptations at least to moisture, pointing to a higher degree of specialization towards disturbance in these habitats, but constituting more the exception than the rule along waterways. Due to the high degree of similar modifications along waterways, specialists became rare and were replaced by generalists (BEJARANO ET AL., 2018; DEILLER ET AL., 2001; HENLE ET AL., 2004), which are mainly competitors with adaptations to stable conditions of mesic moisture levels and low disturbance frequency. Riprap removal along waterways is rather improbable as banks along waterways need to be secured to prevent bank erosion. However, our findings show well that riparian vegetation along front-fixed banks is more similar to typical riparian vegetation than the vegetation along ripraps. Riparian species contribute to a high species turnover of 50% in landscapes, thus enhancing regional biodiversity essentially (SABO ET AL., 2005). To counteract an onward decline of typical riparian species along waterways, restoration measures like the installation of front-fixed banks show high suitability. They enable a certain degree of water level fluctuation but are also suited to prevent bank erosion. Thus, a compromise between concerns of economy and nature conservation can be found by their installation.

2.4.3 Lower species diversity but higher functional diversity at front-fixed and unfortified banks

Diversity levels of ripraps were highest and unfortified banks tended to show a slightly higher diversity than front-fixed banks. Due to the significantly steeper banks of ripraps, the bank structure is very different from front-fixed and unfortified banks, leading to a considerable decrease in flooding dynamics. Steep banks at ripraps consequently lead to a strong moisture gradient in a tight space, thus providing niche space for a broad species spectrum within a relevé. Lower diversity on relevé scale at modified river banks was observed by CAVAILLÉ ET AL. (2013), BISWAS AND MALLIK (2010) and HELFIELD ET AL. (2007), whereas HARVOLK ET AL. (2014), DEILLER ET AL. (2001) and NILSSON ET AL. (1994) revealed higher diversity levels. In fact, our findings show that the occurring species at ripraps have different habitat demands than typical riverine species, thus causing the high diversity levels at modified river banks. By contrast, species typical for riverine habitats and showing better adaptations towards high water availability and more influence of disturbance by flooding mainly occur at front-fixed and unfortified banks, which leads to the question whether the naturalness of habitats can be assessed adequately when only focusing on species diversity. This aspect was also pointed out by DEILLER ET AL. (2001), who showed that flood-tolerant species are replaced by flood-intolerant species, which underlines the meaning of water level fluctuations as important limitation factor in riverine habitats. SABO ET AL. (2005) compared species diversity between terrestrial and riparian habitats and could not find any difference in diversity levels. However, they emphasized the high species turnover in floodplains, which leads to species compositions with different traits than in terrestrial habitats.

Although not significant, the patterns of functional diversity are mostly consistent and tend to be higher at front-fixed and unfortified banks. FRic tended to highest levels in ripraps, indicating higher niche occupation and therefore higher utilization of the available resources, with stronger competitive relationships as a consequence (VILLÉGER ET AL., 2008). This aspect is also well reflected by the high proportion of c-strategists in ripraps. FEve tended to be lower at front-fixed and unfortified banks than at ripraps. Equal availability of resources in niche space provided, it illustrates that not all available resources are used in the same way (MASON ET AL., 2005). This indicates that competition between species becomes less important for the structuring of vegetation and instead differences in site conditions and resource availability gain in importance. While FDiv showed contrasting results, FDis and RaoQ tended to show higher levels at front-fixed and unfortified banks. This reflects greater trait differentiation (LALIBERTÉ AND LEGENDRE, 2010) and therefore larger ecological niche differentiation. Due to lowered resource competition as a consequence of water stress as the major environmental factor niche differentiation should be high at these sites (MASON ET AL., 2005). This is also supported by the strong vertical layering of woody vegetation at these banks. The species composition is therefore characterized by a stronger complementarity in traits, which ensures a more efficient resource use (ABONYI ET AL., 2018) than at ripraps. Our results fit well with MOUILLOT ET AL. (2013), who give orientation for the development of functional diversity indices under increasing disturbance.

With the functional approach we could show that lower species diversity at front-fixed and unfortified banks is not equal with reduced ecosystem functioning. Similar to the NMS results, the reason for the absence of significant relationships might be related to the high regulation degree of the Main and the Danube, which both are impounded. Therefore, riparian species composition at each study site is governed to a higher degree by the surrounding land use than along free-flowing rivers (JOHNSON, 1998). This effect obstructs the detection of differences in species composition that are related to hydrological disturbance. This fact can also be the reason for the still high proportion of c-strategists at front-fixed and unfortified banks, again underlining the impact of river regulation along both rivers. Although the proportion of specialists was higher than along ripraps, their abundance might be not sufficient to raise the levels of functional diversity measures, which were expected to be higher due to improved species adaptation to disturbance by flooding. In comparison to species diversity, functional diversity refers to species traits, which are directly associated to the prevalent environmental processes (BEJARANO ET AL., 2018; GONZÁLEZ ET AL., 2015; MOUILLOT ET AL., 2013), therefore allowing to display them.

2.5 Conclusions

Due to hard embankments and the resulting lack of flooding dynamics, species composition of the banks of waterways mainly consists of species from terrestrial habitats. Although ripraps show the highest species diversity, we showed that trait differentiation tends to be lower than at front-fixed and unfortified banks. In contrast to that, front-fixed and unfortified banks are relatively species-poor, but harbor more characteristic riparian species as these sites are exposed to a higher influence of disturbance by flooding. Moreover, they are suitable to promote biotope cross-linking along waterways, as they are characterized by a strong vertical layering of woody riparian vegetation. Hence, unfortified and front-fixed banks are appropriate to promote characteristic riparian vegetation along waterways. Nature conservation efforts along waterways should therefore focus on the restoration of a higher degree of flooding dynamics and structural diversity. Since a return to unfortified banks due to the maintenance of infrastructure along navigated waterways is rather improbable, the installation of front-fixed banks is a suitable alternative to ripraps. They promote refuge for riparian species at least from backwater habitats in such heavily modified ecosystems like waterways, and they are an attempt to reconnect rivers and their floodplains. Due to their strong vertical layering of woody riparian vegetation, they further contribute to higher habitat diversity. Moreover, they might buffer temperature peaks in summer. Since they combine features suited for the safety of shipping traffic for the promotion of a higher degree of naturalness, they are one example how the concerns of nature conservation and economy can be brought together.

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Appendix Chapter 2

Table A2.1 - Traits used for the calculation of the functional diversity indices, their abbreviation and data origin for the extraction of the respective trait values, their scale level and the specific classification of the traits. Binary variables are signed with 0 when the trait is not found and with 1 when the trait is found.

Trait	Abbreviation	Data origin	Scale	Specification
Guild	LifeForm	BiolFlor	Categorical	Woody (W) Herbaceous (H) Grass (G) Sourgrass (S) Legume (L)
Maximum height	CanHeight	LEDA	Numerical	In meters (m)
Life span	LifeSpan_annual	BiolFlor	Binary	Annuals (one flowering phase)
	LifeSpan_perenn	BiolFlor	Binary	Perennials (more than one flowering phase)
Position of regenerative organ	Regeneration	Ellenberg	Categorical	Aboveground (a) Belowground (b) Therophyte (T)
Ecological optimum for moisture	EIV_moisture	Ellenberg	Categorical	Values between 1 and 10 (1 = dry site conditions to 10 = aquatic plants)
Tolerance for periodic wetness	Periodic_wet	Ellenberg	Binary	Ellenberg Indicator value – additional humidity value for periodic wetness
Flooding tolerance	Flooding	Ellenberg	Binary	Ellenberg Indicator value – additional humidity value for flooding

Table A2.2 - Categories, environmental variables, their short name and units that were used for NMS.

Category	Variable	Shortname	Unit
Topography	Altitude	Altitude	m
	Inclination banks	Inclin	%
Vegetation	Cover tree layer	Cover tree	%
	Cover shrub layer	Cover shrubs	%
	Cover herb layer	Cover herbs	%
	Cover grass layer	Cover grass	%
	Cover litter layer	Cover litter	%
	Cover open soil	Cover soil	%
Species diversity	Richness	Richness	Unitless
	Shannon index	Shannon	Unitless
	Evenness	Evenness	Unitless
Local site conditions	Mean Ellenberg indicator value (Light)	EIV Light	Unitless
	Mean Ellenberg indicator value (Moisture)	EIV Moisture	Unitless
	Average number of flooding days for each bank type	Number flooding days	d
	Lime content soil	$CaCO_3$	%
	Phosphorous content soil	P_2O_5	g kg $^{-1}$
	Potassium content soil	K_2O	g kg $^{-1}$
	Total nitrogen content soil	Ntot	%

Table A2.3 - Correlations of environmental variables with ordination axes used of each NMS.

Waterway	Environmental variable	Axis 1 R^2	Axis 2 R^2	Axis 3 R^2
Main and Danube Rivers	Altitude	0.799	0.033	0.010
	Inclin	0.008	0.099	0.213
	Cover trees	0.004	0.093	0.030
	Cover shrubs	0.094	0.017	0.053
	Cover herbs	0.306	0.020	0.052
	Cover litter	0.166	0.122	0.001
	Cover soil	0.001	0.034	0.086
	Cover grass	0.347	0.039	0.138
	Richness	0.016	0.281	0.111
	Shannon	0.021	0.273	0.154
	Evenness	0.030	0.114	0.075
	EIV Light	0.039	0.197	0.005
	EIV Moisture	0.258	0.130	0.064
	Number flooding days	0.238	0.068	0.074
	$CaCO_3$	0.588	0.088	0.000
	P_2O_5	0.419	0.002	0.021
	K_2O	0.149	0.003	0.000
	Ntot	0.080	0.103	0.034
Main River	Altitude	0.566	0.092	0.031
	Inclin	0.074	0.312	0.052
	Cover trees	0.116	0.008	0.157
	Cover shrubs	0.185	0.040	0.188
	Cover herbs	0.122	0.000	0.103
	Cover litter	0.233	0.001	0.102
	Cover soil	0.092	0.014	0.079
	Cover grass	0.353	0.010	0.041
	Richness	0.241	0.035	0.337
	Shannon	0.218	0.001	0.292
	Evenness	0.047	0.016	0.018
	EIV Light	0.363	0.118	0.012
	EIV Moisture	0.388	0.008	0.101
	Number flooding days	0.241	0.000	0.068
	$CaCO_3$	0.109	0.008	0.002
	P_2O_5	0.099	0.018	0.010
	K_2O	0.102	0.087	0.157
	Ntot	0.172	0.008	0.178
Danube River	Altitude	0.020	0.001	0.005
	Inclin	0.035	0.001	0.109
	Cover trees	0.032	0.251	0.112
	Cover shrubs	0.006	0.197	0.006
	Cover herbs	0.144	0.149	0.011
	Cover litter	0.033	0.021	0.192
	Cover soil	0.016	0.126	0.014
	Cover grass	0.065	0.348	0.002
	Richness	0.060	0.335	0.285
	Shannon	0.057	0.370	0.427
	Evenness	0.031	0.010	0.313
	EIV Light	0.021	0.011	0.184
	EIV Moisture	0.175	0.001	0.001
	Number flooding days	0.263	0.270	0.000

$CaCO_3$	0.000	0.006	0.036
P_2O_5	0.005	0.244	0.004
K_2O	0.003	0.007	0.035
Ntot	0.000	0.099	0.002

Table A2.4 - Results of the soil chemical analyses (mean ± standard deviation) for each river and bank type (riprap (R), front-fixed (F), unfortified (U)). Asterisks mark the significance level (*p < 0.05; ** p < 0.01; *** p < 0.001) detected by a Kruskal-Wallis test in Statistica 13. Similar letters indicate homogenous groups according to Mann-Whitney-U-Test (p < 0.05).

	Main			Danube		
	R (n=16)	F (n=15)	U (n=16)	R (n=16)	F (n=15)	U (n=16)
pH (aqua dest.)	7.76 ± 0.15	7.72 ± 0.24	7.76 ± 0.18	8.12 ± 0.16	8.17 ± 0.21	8.21 ± 0.17
pH (KCl)	7.22 ± 0.11	7.29 ± 0.32	7.30 ± 0.28	7.36 ± 0.06	7.43 ± 0.16	7.47 ± 0.26
$CaCO_3$ (%)*	4.61 ± 1.88	3.91 ± 1.60	3.40 ± 1.95	23.38 ± 1.43 a	20.28 ± 4.68 ab	17.58 ± 63.50 b
P_2O_5 (g kg^{-1})	368.06 ± 98.27	350.01 ± 210.68	329.79 ± 178.61	179.06 ± 90.29	166.56 ± 59.60	165.04 ± 63.64
K_2O (g kg^{-1})**	171.61 ± 104.95	147.56 ± 130.79	157.99 ± 81.25	150.84 ± 47.47 a	93.09 ± 29.13 b	93.98 ± 34.42 b
N_{total} (%) **	0.19 ± 0.06	0.18 ± 0.10	0.15 ± 0.07	0.29 ± 0.05 a	0.26 ± 0.05 ab	0.20 ± 0.07 b
C_{total} (%)***	2.92 ± 0.99	2.63 ± 1.36	2.21 ± 1.10	7.04 ± 0.50 a	6.21 ± 0.86 ab	4.99 ± 1.67 b
C/N	15.75 ± 1.75	15.07 ± 2.26	14.81 ± 2.94	25.06 ± 2.86	24.27 ± 2.98	24.50 ± 2.81
C_{org} (%)***	2.37 ± 0.86	2.16 ± 1.29	1.80 ± 0.90	4.23 ± 0.54 a	3.78 ± 0.61 ab	2.88 ± 1.02 b
C_{anorg} (%)*	0.55 ± 0.23	0.47 ± 0.19	0.41 ± 0.23	2.81 ± 0.17 a	2.43 ± 0.56 ab	1.98 ± 0.82 b

Table A2.5 - Results of the indicator species analysis for the bank types (riprap (R; n=16), front-fixed (F; n=15), unfortified (U; n=16)) and the combinations of bank types for the Main-River. Significant indicator species are characterised by an indicator value (IV) >25 and a p-value <0.05 (Monte Carlo randomization test).

Bank type	Full species name	A (Specificity)	B (Sensitivity)	IV	p.value	Significance
R	*Salix purpurea*	0.9071	0.625	0.753	0.001	***
	Geranium pratense	0.7413	0.625	0.681	0.005	**
	Barbarea vulgaris	0.9292	0.3125	0.539	0.007	**
	Iris pseudacorus	0.9167	0.3125	0.535	0.016	*
	Lamium album	0.8678	0.3125	0.521	0.017	*
	Scrophularia auriculata	0.9062	0.3125	0.532	0.018	*
	Acer pseudoplatanus	1	0.25	0.500	0.028	*
	Ranunculus acris	0.7317	0.3125	0.478	0.048	*
	Galium mollugo	0.7207	0.3125	0.475	0.137	
	Festuca pratensis	0.8333	0.1875	0.395	0.139	
	Vicia cracca	0.7588	0.25	0.436	0.175	
	Vicia sepium	0.8242	0.1875	0.393	0.182	
	Galium verum	1	0.125	0.354	0.325	
	Raphanus sativus	1	0.125	0.354	0.326	
	Anthriscus sylvestris	1	0.125	0.354	0.33	
	Clematis vitalba	1	0.125	0.354	0.33	
	Parthenocissus quinquefolia	1	0.125	0.354	0.343	
	Aristolochia clematitis	1	0.125	0.250	1	
	Bromus inermis	1	0.0625	0.250	1	
	Calamagrostis epigejos	1	0.0625	0.250	1	

	Dactylis polygama	1	0.0625	0.250	1	
	Geranium molle	1	0.0625	0.250	1	
	Hypericum maculatum	1	0.0625	0.250	1	
	Parthenocissus inserta	1	0.0625	0.250	1	
	Poa pratensis	1	0.0625	0.250	1	
	Populus trichocarpa	1	0.0625	0.250	1	
	Quercus robur	1	0.0625	0.250	1	
	Ranunculus repens	1	0.0625	0.250	1	
	Rapistrum rugosum	1	0.0625	0.250	1	
	Salix viminalis	1	0.0625	0.250	1	
	Silene dioica	1	0.0625	0.250	1	
	Sisymbrium officinale	1	0.0625	0.250	1	
	Vicia villosa	1	0.0625	0.250	1	
F	*Salix eleagnos*	1	0.2	0.447	0.027	*
	Epilobium parviflorum	1	0.2	0.447	0.037	*
	Salix fragilis	0.9589	0.2	0.438	0.046	*
	Lysimachia vulgaris	1	0.13333	0.365	0.106	
	Acer campestre	1	0.13333	0.365	0.111	
	Carex hirta	0.72727	0.2	0.381	0.148	
	Tilia platyphyllos	1	0.06667	0.258	0.305	
	Glyceria maxima	1	0.06667	0.258	0.311	
	Potentilla anserina	1	0.06667	0.258	0.311	
	Bromus sterilis	1	0.06667	0.258	0.321	
	Ulmus minor	1	0.06667	0.258	0.321	
	Heracleum sphondylium	1	0.06667	0.258	0.322	
	Carduus nutans	1	0.06667	0.258	0.328	
	Cirsium oleraceum	1	0.06667	0.258	0.328	
	Cerastium glomeratum	1	0.06667	0.258	0.333	
	Rorippa pyrenaica	1	0.06667	0.258	0.333	
	Juncus conglomeratus	1	0.06667	0.258	0.335	
	Rorippa anceps	1	0.06667	0.258	0.335	
	Trifolium pratense	1	0.06667	0.258	0.335	
	Stachys annua	1	0.06667	0.258	0.341	
U	*Thalictrum flavum*	0.6738	0.3125	0.459	0.151	
	Atriplex patula	1	0.125	0.354	0.302	
	Sambucus nigra	1	0.125	0.354	0.309	
	Erysimum cuspidatum	1	0.125	0.354	0.326	
	Impatiens glandulifera	0.7769	0.1875	0.382	0.401	
	Achillea ptarmica	1	0.0625	0.250	1	
	Agrimonia eupatoria	1	0.0625	0.250	1	
	Centaurea nigrescens	1	0.0625	0.250	1	
	Cirsium tuberosum	1	0.0625	0.250	1	
	Persicaria hydropiper	1	0.0625	0.250	1	
	Rumex acetosella	1	0.0625	0.250	1	
	Salix rosmarinifolia	1	0.0625	0.250	1	
	Viola hirta	1	0.0625	0.250	1	

R+F	*Arrhenatherum elatius*	0.90279	0.41935	0.615	0.077	.
	Cirsium arvense	1	0.25806	0.508	0.088	.
	Lycopus europaeus	0.86111	0.41935	0.601	0.109	
	Rumex thyrsiflorus	1	0.19355	0.440	0.176	
	Symphytum officinale	0.96314	0.22581	0.466	0.193	
	Mentha longifolia	1	0.16129	0.402	0.261	
	Sonchus asper	1	0.16129	0.402	0.283	
	Rumex sanguineus	0.87854	0.19355	0.412	0.306	
	Valeriana procurrens	0.92701	0.19355	0.424	0.357	
	Ribes rubrum	1	0.12903	0.359	0.415	
	Silene latifolia	0.89399	0.19355	0.416	0.502	
	Lotus corniculatus	1	0.09677	0.311	0.511	
	Melilotus indicus	1	0.09677	0.311	0.514	
	Rumex crispus	0.95588	0.12903	0.351	0.515	
	Capsella bursa-pastoris	1	0.09677	0.311	0.515	
	Melilotus officinalis	0.93182	0.12903	0.347	0.55	
	Sisymbrium volgense	1	0.06452	0.254	0.738	
	Equisetum arvense	1	0.06452	0.254	0.755	
	Acer platanoides	1	0.06452	0.254	0.766	
	Juncus filiformis	1	0.06452	0.254	0.775	
R+U	*Elymus repens*	0.94142	0.4375	0.642	0.051	.
	Glechoma hederacea	0.83142	0.53125	0.665	0.099	.
	Angelica archangelica	0.94216	0.3125	0.543	0.131	
	Rosa canina	1	0.1875	0.433	0.225	
	Sanguisorba minor	1	0.1875	0.433	0.257	
	Festuca rubra	1	0.1875	0.433	0.26	
	Mentha aquatica	0.90062	0.25	0.475	0.309	
	Anchusa officinalis	1	0.15625	0.395	0.353	
	Cardamine impatiens	1	0.15625	0.395	0.359	
	Lepidium campestre	1	0.09375	0.306	0.755	
	Rorippa amphibia	1	0.09375	0.306	0.761	
	Berteroa incana	1	0.09375	0.306	0.78	
	Rhamnus cathartica	1	0.0625	0.250	1	
	Vicia sativa	1	0.0625	0.250	1	
F+U	*Humulus lupulus*	0.92029	0.41935	0.621	0.045	*
	Lolium perenne	1	0.22581	0.475	0.121	
	Impatiens parviflora	0.87817	0.29032	0.505	0.185	
	Impatiens noli-tangere	0.92174	0.19355	0.422	0.234	
	Plantago lanceolata	0.91228	0.22581	0.454	0.282	
	Nepeta cataria	0.87539	0.22581	0.445	0.33	
	Festuca gigantea	0.81337	0.29032	0.486	0.395	
	Galeopsis pubescens	1	0.12903	0.359	0.433	
	Acer negundo	1	0.12903	0.359	0.442	
	Plantago media	1	0.12903	0.359	0.446	
	Trifolium dubium	1	0.12903	0.359	0.447	
	Prunus padus	1	0.09677	0.311	0.687	
	Trifolium repens	1	0.06452	0.254	0.759	

Convolvulus arvensis	1	0.06452	0.254	0.762
Euphorbia cyparissias	1	0.06452	0.254	0.77
Arctium lappa	1	0.06452	0.254	0.772
Lamium maculatum	0.89387	0.12903	0.340	0.835

Table A2.6 - Species without specific bank type association at the Main River (determined by indicator species analysis). R=riprap, F=front-fixed, U=unfortified, IV=indicator value, index=7 refers to the combination of all three study sites.

Species name	R	F	U	index	IV	p.value
Achillea millefolium	1	1	1	7	0.48377945	NA
Aegopodium podagraria	1	1	1	7	0.48377945	NA
Alliaria petiolata	1	1	1	7	0.4612656	NA
Alnus glutinosa	1	1	1	7	0.4125685	NA
Alopecurus pratensis	1	1	1	7	0.54577682	NA
Arctium minus	1	1	1	7	0.3572948	NA
Artemisia vulgaris	1	1	1	7	0.60141677	NA
Ballota nigra	1	1	1	7	0.29172998	NA
Barbarea stricta	1	1	1	7	0.25264558	NA
Calystegia sepium	1	1	1	7	0.83793058	NA
Carduus crispus	1	1	1	7	0.25264558	NA
Carex acuta	1	1	1	7	0.25264558	NA
Chaerophyllum aureum	1	1	1	7	0.75793673	NA
Cornus sanguinea	1	1	1	7	0.54577682	NA
Crataegus monogyna	1	1	1	7	0.50529115	NA
Dactylis glomerata	1	1	1	7	0.7145896	NA
Elymus caninus	1	1	1	7	0.3572948	NA
Equisetum × litorale	1	1	1	7	0.29172998	NA
Filipendula ulmaria	1	1	1	7	0.63581076	NA
Fraxinus excelsior	1	1	1	7	0.4125685	NA
Galium aparine	1	1	1	7	0.7145896	NA
Geum urbanum	1	1	1	7	0.56493268	NA
Hedera helix	1	1	1	7	0.32616404	NA
Leucanthemum ircutianum	1	1	1	7	0.29172998	NA
Lythrum salicaria	1	1	1	7	0.61885275	NA
Mentha × verticillata	1	1	1	7	0.29172998	NA
Papaver rhoeas	1	1	1	7	0.29172998	NA
Phalaris arundinacea	1	1	1	7	0.83793058	NA
Phragmites australis	1	1	1	7	0.48377945	NA
Poa annua	1	1	1	7	0.29172998	NA
Poa palustris	1	1	1	7	0.69954392	NA
Poa trivialis	1	1	1	7	0.56493268	NA
Populus nigra	1	1	1	7	0.25264558	NA
Potentilla reptans	1	1	1	7	0.43759497	NA
Ficaria verna	1	1	1	7	0.63581076	NA
Rubus caesius	1	1	1	7	0.7145896	NA
Salix alba	1	1	1	7	0.58345997	NA
Salix triandra	1	1	1	7	0.4125685	NA

Solanum dulcamara	1	1	1	7	0.58345997	NA
Tanacetum vulgare	1	1	1	7	0.3572948	NA
Taraxacum sect. Ruderalia	1	1	1	7	0.43759497	NA
Urtica dioica	1	1	1	7	0.8991722	NA
Valeriana officinalis	1	1	1	7	0.29172998	NA
Vicia hirsuta	1	1	1	7	0.32616404	NA

Table A2.7 - Results of the indicator species analysis for the bank types (riprap (R; n=16), front-fixed (F; n=15), unfortified (U; n=16)) and the combinations of bank types for the Danube-River. Significant indicator species are characterised by an indicator value (IV) >25 and a p-value <0.05 (Monte Carlo randomization test).

Bank type	Full species name	A (Specificity)	B (Sensitivity)	IV	p.value	Significance
R	*Angelica archangelica*	0.9575	0.4375	0.647	0.001	***
	Solanum dulcamara	0.8846	0.4375	0.622	0.003	**
	Sanguisorba officinalis	0.8	0.25	0.447	0.062	.
	Fraxinus excelsior	0.8579	0.3125	0.518	0.077	.
	Bromus tectorum	0.8	0.25	0.447	0.078	.
	Myosotis laxa	1	0.1875	0.433	0.09	.
	Galium verum	1	0.1875	0.433	0.103	
	Festuca rubra	0.6791	0.4375	0.545	0.131	
	Sedum acre	0.7586	0.25	0.435	0.202	
	Lathyrus pratensis	0.5876	0.5	0.542	0.225	
	Agrostis vinealis	1	0.125	0.354	0.294	
	Rumex thyrsiflorus	1	0.125	0.354	0.313	
	Hypericum perforatum	1	0.125	0.354	0.326	
	Melilotus altissimus	1	0.125	0.354	0.335	
	Linaria vulgaris	1	0.125	0.354	0.344	
	Prunus spinosa	0.8242	0.125	0.321	0.542	
	Achillea ptarmica	0.7269	0.125	0.301	0.613	
	Corylus avellana	1	0.0625	0.25	1	
	Echinops sphaerocephalus	1	0.0625	0.25	1	
	Elymus caninus	1	0.0625	0.25	1	
	Filipendula vulgaris	1	0.0625	0.25	1	
	Fragaria viridis	1	0.0625	0.25	1	
	Melilotus albus	1	0.0625	0.25	1	
	Potentilla anserina	1	0.0625	0.25	1	
	Rorippa pyrenaica	1	0.0625	0.25	1	
	Sambucus nigra	1	0.0625	0.25	1	
	Sanguisorba minor	1	0.0625	0.25	1	
	Securigera varia	1	0.0625	0.25	1	
F	*Deschampsia cespitosa*	1	0.26667	0.516	0.007	**
	Glechoma hederacea	0.91429	0.2	0.428	0.057	.
	Geum urbanum	1	0.13333	0.365	0.109	
	Carex acuta	0.88189	0.13333	0.343	0.143	
	Epilobium ciliatum	0.7619	0.13333	0.319	0.177	
	Vicia villosa	0.7619	0.13333	0.319	0.205	

	Viburnum lantana	1	0.06667	0.258	0.288	
	Acer pseudoplatanus	1	0.06667	0.258	0.306	
	Ribes rubrum	1	0.06667	0.258	0.321	
	Cornus sanguinea	1	0.06667	0.258	0.327	
	Verbena officinalis	1	0.06667	0.258	0.33	
	Poa trivialis	1	0.06667	0.258	0.335	
	Vicia angustifolia	1	0.06667	0.258	0.335	
	Betula pendula	1	0.06667	0.258	0.345	
	Trifolium pratense	1	0.06667	0.258	0.345	
	Phragmites australis	0.78873	0.2	0.397	0.388	
U	*Silene vulgaris*	0.7721	0.3125	0.491	0.033	*
	Mentha longifolia	0.85	0.25	0.461	0.071	.
	Rumex conglomeratus	1	0.1875	0.433	0.096	.
	Scrophularia umbrosa	0.7746	0.25	0.44	0.098	.
	Juncus effusus	1	0.125	0.354	0.3	
	Rumex aquaticus	1	0.125	0.354	0.311	
	Rorippa anceps	1	0.125	0.354	0.312	
	Lolium perenne	0.859	0.125	0.328	0.314	
	Melilotus officinalis	1	0.125	0.354	0.318	
	Veronica maritima	1	0.125	0.354	0.333	
	Rorippa amphibia	1	0.125	0.354	0.333	
	Medicago falcata	0.7857	0.125	0.313	0.403	
	Acer negundo	1	0.0625	0.25	1	
	Arctium minus	1	0.0625	0.25	1	
	Capsella bursa-pastoris	1	0.0625	0.25	1	
	Cirsium vulgare	1	0.0625	0.25	1	
	Daucus carota	1	0.0625	0.25	1	
	Festuca gigantea	1	0.0625	0.25	1	
	Glyceria maxima	1	0.0625	0.25	1	
	Lapsana communis	1	0.0625	0.25	1	
	Mentha spicata	1	0.0625	0.25	1	
	Rosa multiflora	1	0.0625	0.25	1	
	Rumex sanguineus	1	0.0625	0.25	1	
	Salix caesia	1	0.0625	0.25	1	
	Taraxacum sect. Ruderalia	1	0.0625	0.25	1	
	Trifolium dubium	1	0.0625	0.25	1	
	Ulmus minor	1	0.0625	0.25	1	
	Valeriana procurrens	1	0.0625	0.25	1	
	Veronica catenata	1	0.0625	0.25	1	
R+F	*Potentilla reptans*	0.88848	0.35484	0.561	0.16	
	Salix alba	0.92797	0.16129	0.387	0.455	
	Salix viminalis	0.9589	0.12903	0.352	0.595	
	Vicia sepium	1	0.09677	0.311	0.605	
	Juglans regia	1	0.09677	0.311	0.624	
	Lonicera xylosteum	1	0.06452	0.254	0.756	
	Acer campestre	1	0.06452	0.254	0.775	
	Trifolium repens	1	0.06452	0.254	0.788	

R+U	*Galium mollugo*	0.95541	0.75	0.846	0.001	***
	Arrhenatherum elatius	0.91881	0.75	0.83	0.001	***
	Elymus repens	0.80928	0.53125	0.656	0.088	.
	Salix fragilis	1	0.21875	0.468	0.156	
	Lysimachia vulgaris	1	0.1875	0.433	0.189	
	Chaerophyllum bulbosum	1	0.21875	0.468	0.19	
	Thalictrum minus	1	0.1875	0.433	0.228	
	Salix purpurea	0.93036	0.25	0.482	0.325	
	Saponaria officinalis	1	0.15625	0.395	0.342	
	Lycopus europaeus	1	0.15625	0.395	0.343	
	Plantago lanceolata	0.84906	0.3125	0.515	0.352	
	Vicia tetrasperma	1	0.15625	0.395	0.352	
	Agrimonia procera	0.82418	0.1875	0.393	0.687	
	Rumex acetosa	1	0.09375	0.306	0.761	
	Barbarea intermedia	1	0.09375	0.306	0.762	
	Euphorbia platyphyllos	1	0.09375	0.306	0.779	
	Thalictrum flavum	0.87302	0.125	0.33	0.817	
	Rumex hydrolapathum	1	0.0625	0.25	1	
F+U	*Iris pseudacorus*	0.94106	0.35484	0.578	0.032	*
	Impatiens glandulifera	0.90083	0.35484	0.565	0.127	
	Bromus inermis	0.86607	0.19355	0.409	0.471	
	Agrostis canina	1	0.09677	0.311	0.616	
	Agrostis capillaris	1	0.09677	0.311	0.64	
	Juncus articulatus	1	0.06452	0.254	0.744	
	Viburnum opulus	1	0.06452	0.254	0.748	
	Crataegus monogyna	1	0.06452	0.254	0.756	
	Alopecurus pratensis	1	0.06452	0.254	0.759	
	Achillea millefolium	1	0.06452	0.254	0.766	
	Agrostis stolonifera	1	0.06452	0.254	0.771	
	Scrophularia nodosa	1	0.06452	0.254	0.777	
	Lotus corniculatus	1	0.06452	0.254	0.778	

Table A2.8 - Species without specific bank type association at the Danube River (determined by indicator species analysis). R=riprap, F=front-fixed, U=unfortified, IV=indicator value, index=7 refers to the combination of all three study sites.

Species name	R	F	U	index	IV	p.value
Alnus glutinosa	1	1	1	7	0.68416745	NA
Calamagrostis epigejos	1	1	1	7	0.54577682	NA
Calystegia sepium	1	1	1	7	0.43759497	NA
Calystegia silvatica	1	1	1	7	0.63581076	NA
Carex hirta	1	1	1	7	0.50529115	NA
Cirsium arvense	1	1	1	7	0.32616404	NA
Cornus alba	1	1	1	7	0.54577682	NA
Dactylis glomerata	1	1	1	7	0.7145896	NA
Equisetum arvense	1	1	1	7	0.43759497	NA
Festuca arundinacea	1	1	1	7	0.95650071	NA
Filipendula ulmaria	1	1	1	7	0.8121419	NA

Galeopsis pubescens	1	1	1	7	0.38592249	NA
Galium aparine	1	1	1	7	0.58345997	NA
Humulus lupulus	1	1	1	7	0.25264558	NA
Lythrum salicaria	1	1	1	7	0.4125685	NA
Phalaris arundinacea	1	1	1	7	0.77184498	NA
Phleum pratense	1	1	1	7	0.38592249	NA
Poa palustris	1	1	1	7	0.92253121	NA
Rubus caesius	1	1	1	7	0.83793058	NA
Scutellaria galericulata	1	1	1	7	0.52592371	NA
Solidago canadensis	1	1	1	7	0.61885275	NA
Urtica dioica	1	1	1	7	0.83793058	NA
Valeriana officinalis	1	1	1	7	0.50529115	NA
Vicia cracca	1	1	1	7	0.65232807	NA

Table A2.9 - Site-associated species with the respective Ellenberg indicator value (EIV) for light and moisture that were used in the trait analysis for each bank type (riprap (R), front-fixed (F), unfortified (U)) and waterway. The higher the EIV, the higher the demand for light and moisture of the species. Species marked with an “x” do not react to a change in light or moisture conditions. Species, for which an EIV was not available are characterized with “NA” (=not available) and categorized as “Other” (no statistical consideration).

			Main River			Danube River		
	Bank type	Classification	Species	EIV	Percentage	Species	EIV	Percentage
EIV (Light)	R	>5	*Aristolochia clematitis*	6	86.7	*Corylus avellana*	6	92.0
			Poa pratensis	6		*Angelica archangelica*	7	
			Ranunculus repens	6		*Filipendula vulgaris*	7	
			Raphanus sativus	6		*Fragaria viridis*	7	
			Anthriscus sylvestris	6		*Galium verum*	7	
			Calamagrostis epigejos	7		*Hypericum perforatum*	7	
			Clematis vitalba	7		*Lathyrus pratensis*	7	
			Galium album	7		*Myosotis laxa*	7	
			Galium verum	7		*Potentilla anserina*	7	
			Geranium molle	7		*Sambucus nigra*	7	
			Iris pseudacorus	7		*Sanguisorba minor*	7	
			Lamium album	7		*Sanguisorba officinalis*	7	
			Quercus robur	7		*Securigera varia*	7	
			Ranunculus acris	7		*Solanum dulcamara*	7	
			Rapistrum rugosum	7		*Achillea ptarmica*	8	
			Salix viminalis	7		*Bromus tectorum*	8	
			Vicia cracca	7		*Echinops sphaerocephalus*	8	
			Vicia villosa	7		*Linaria vulgaris*	8	
			Barbarea vulgaris	7		*Melilotus altissimus*	8	
			Bromus inermis	8		*Rorippa pyrenaica*	8	
			Festuca pratensis	8		*Rumex thyrsiflorus*	8	
			Geranium pratense	8		*Sedum acre*	8	
			Hypericum maculatum	8		*Melilotus albus*	9	
			Salix purpurea	8				
			Scrophularia auriculata	8				

		Sisymbrium officinale	8				
			8				
	≤5	*Acer pseudoplatanus*	4	6.7	*Fraxinus excelsior*	4	4.0
		Dactylis polygama	5				
	Indifferent	*Silene dioica*	x	6.7	*Festuca rubra*	x	4.0
		Vicia sepium	x				
	Other	*Parthenocissus inserta*	NA	-	*Agrostis vinealis*	NA	-
		Parthenocissus quinquefolia	NA		*Elymus caninus*	NA	
		Populus trichocarpa	NA		*Prunus spinosa*	NA	
F	>5	*Lysimachia vulgaris*	6	80.0	*Deschampsia cespitosa*	6	71.4
		Cirsium oleraceum	6		*Glechoma hederacea*	6	
		Bromus sterilis	7		*Poa trivialis*	6	
		Carex hirta	7		*Betula pendula*	7	
		Cerastium glomeratum	7		*Cornus sanguinea*	7	
		Epilobium parviflorum	7		*Phragmites australis*	7	
		Heracleum sphondylium	7		*Trifolium pratense*	7	
		Potentilla anserina	7		*Viburnum lantana*	7	
		Rorippa anceps	7		*Vicia villosa*	7	
		Salix eleagnos	7		*Verbena officinalis*	9	
		Stachys annua	7				
		Trifolium pratense	7				
		Carduus nutans	8				
		Juncus conglomeratus	8				
		Rorippa pyrenaica	8				
		Glyceria maxima	9				
	≤ 5	*Tilia platyphyllos*	4	20.0	*Acer pseudoplatanus*	4	28.6
		Acer campestre	5		*Geum urbanum*	4	
		Salix fragilis	5		*Ribes rubrum*	4	
		Ulmus minor	5		*Vicia angustifolia*	5	

	Indifferent	-		0	-		
	Other	-			*Carex acuta*	NA	
					Epilobium ciliatum	NA	
U	>5	*Atriplex patula*	6	91.0	*Trifolium dubium*	6	80.8
		Viola hirta	6		*Capsella bursa-pastoris*	7	
		Agrimonia eupatoria	7		*Mentha longifolia*	7	
		Cirsium tuberosum	7		*Rorippa amphibia*	7	
		Sambucus nigra	7		*Rorippa anceps*	7	
		Thalictrum flavum	7		*Rumex aquaticus*	7	
		Achillea ptarmica	8		*Scrophularia umbrosa*	7	
		Centaurea nigrescens	8		*Taraxacum sect. Ruderalia*	7	
		Rumex acetosella	8		*Valeriana procurrens*	7	
		Salix rosmarinifolia	8		*Veronica maritima*	7	
					Cirsium vulgare	8	
					Daucus carota	8	
					Juncus effusus	8	
					Lolium perenne	8	
					Medicago falcata	8	
					Melilotus officinalis	8	
					Rumex conglomeratus	8	
					Silene vulgaris	8	
					Veronica catenata	8	
					Arctium minus	9	
					Glyceria maxima	9	
	≤5	*Impatiens glandulifera*	5	9.0	*Festuca gigantea*	4	19.2
					Rumex sanguineus	4	
					Acer negundo	5	
					Lapsana communis	5	
					Ulmus minor	5	
	Other	-		0	-		0

		Other	*Erysimum cuspidatum*	NA	-	*Mentha spicata*	NA	-
			Persicaria hydropiper	NA		*Rosa multiflora*	NA	
						Salix caesia	NA	
EIV (Moisture)	R	>6	*Ranunculus repens*	7	13.3	*Melilotus altissimus*	7	20.0
			Salix viminalis	8		*Achillea ptarmica*	8	
			Iris pseudacorus	9		*Solanum dulcamara*	8	
			Scrophularia auriculata	9		*Angelica archangelica*	9	
						Myosotis laxa	9	
		≤6	*Aristolochia clematitis*	4	73.3	*Sedum acre*	2	72.0
			Bromus inermis	4		*Bromus tectorum*	3	
			Galium verum	4		*Filipendula vulgaris*	3	
			Geranium molle	4		*Fragaria viridis*	3	
			Rapistrum rugosum	4		*Melilotus albus*	3	
			Sisymbrium officinale	4		*Rumex thyrsiflorus*	3	
			Vicia villosa	4		*Sanguisorba minor*	3	
			Anthriscus sylvestris	5		*Echinops sphaerocephalus*	4	
			Clematis vitalba	5		*Galium verum*	4	
			Dactylis polygama	5		*Hypericum perforatum*	4	
			Galium album	5		*Linaria vulgaris*	4	
			Geranium pratense	5		*Securigera varia*	4	
			Lamium album	5		*Rorippa pyrenaica*	5	
			Raphanus sativus	5		*Sambucus nigra*	5	
			Poa pratensis	5		*Festuca rubra*	6	
			Vicia sepium	5		*Lathyrus pratensis*	6	
			Barbarea vulgaris	6		*Potentilla anserina*	6	
			Festuca pratensis	6		*Sanguisorba officinalis*	6	
			Hypericum maculatum	6				
			Ranunculus acris	6				
			Silene dioica	6				
			Vicia cracca	6				

	Indifferent	*Acer pseudoplatanus*	x	13.3		*Corylus avellana*	x	8.0
		Calamagrostis epigejos	x			*Fraxinus excelsior*	x	
		Quercus robur	x					
		Salix purpurea	x					
	Other	*Parthenocissus inserta*	NA	-	NA	*Agrostis vinealis*	NA	-
		Parthenocissus quinquefolia	NA		NA	*Elymus caninus*	NA	
		Populus trichocarpa	NA		NA	*Prunus spinosa*	NA	
F	>6	*Cirsium oleraceum*	7	40.0		*Deschampsia cespitosa*	7	28.6
		Juncus conglomeratus	7			*Poa trivialis*	7	
		Salix eleagnos	7			*Ribes rubrum*	8	
		Lysimachia vulgaris	8			*Phragmites australis*	10	
		Salix fragilis	8					
		Epilobium parviflorum	9					
		Rorippa anceps	9					
		Glyceria maxima	10					
	≤6	*Stachys annua*	3	55.0		*Viburnum lantana*	4	50.0
		Bromus sterilis	4			*Vicia villosa*	4	
		Acer campestre	5			*Cornus sanguinea*	5	
		Cerastium glomeratum	5			*Geum urbanum*	5	
		Heracleum sphondylium	5			*Trifolium pratense*	5	
		Rorippa pyrenaica	5			*Verbena officinalis*	5	
		Trifolium pratense	5			*Glechoma hederacea*	6	
		Carex hirta	6					
		Carduus nutans	6					
		Tilia platyphyllos	6					
		Potentilla anserina	6					
	Indifferent	*Ulmus minor*	x	5		*Acer pseudoplatanus*	x	21.4
						Betula pendula	x	
						Vicia angustifolia	x	
	Other	-		-		*Carex acuta*		-

					Epilobium ciliatum		
U	>6	*Achillea ptarmica*	8	36.4	*Festuca gigantea*	7	50.0
		Impatiens glandulifera	8		*Juncus effusus*	7	
		Salix rosmarinifolia	8		*Rumex conglomeratus*	7	
		Thalictrum flavum	8		*Mentha longifolia*	8	
					Rumex aquaticus	8	
					Rumex sanguineus	8	
					Valeriana procurrens	8	
					Veronica maritima	8	
					Rorippa anceps	9	
					Scrophularia umbrosa	9	
					Veronica catenata	9	
					Glyceria maxima	10	
					Rorippa amphibia	10	
	≤6	*Rumex acetosella*	3	63.3	*Medicago falcata*	3	46.2
		Viola hirta	3		*Melilotus officinalis*	3	
		Agrimonia eupatoria	4		*Daucus carota*	4	
		Centaurea nigrescens	4		*Silene vulgaris*	4	
		Atriplex patula	5		*Trifolium dubium*	4	
		Sambucus nigra	5		*Arctium minus*	5	
		Cirsium tuberosum	6		*Capsella bursa-pastoris*	5	
					Cirsium vulgare	5	
					Lapsana communis	5	
					Lolium perenne	5	
					Taraxacum sect. Ruderalia	5	
					Acer negundo	6	
	Indifferent	-		0	*Ulmus minor*	x	3.8
	Other	*Erysimum cuspidatum*	NA	-	*Mentha spicata*	NA	-
		Persicaria hydropiper	NA		*Rosa multiflora*	NA	
					Salix caesia	NA	

Table A2.10 - Site-associated species shown by its biotope origin (limnic, terrestrial, limnic and terrestrial) for each bank type (riprap (R), front-fixed (F), unfortified (U)) and waterway which were used in the trait analysis as well as the percentage of each group as part of the whole group.

Bank type	Classification	Main River	Percentage	Danube River	Percentage
R	Limnic biotope species	*Iris pseudacorus*	12.0	*Achillea ptarmica*	11.0
		Salix purpurea		*Angelica archangelica*	
		Salix viminalis		*Elymus caninus*	
		Scrophularia auriculata			
	Terrestrial biotope species	*Anthriscus sylvestris*	32.0	*Agrostis vinealis*	57.0
		Bromus inermis		*Bromus tectorum*	
		Dactylis polygama		*Echinops sphaerocephalus*	
		Festuca pratensis		*Festuca rubra*	
		Galium verum		*Filipendula vulgaris*	
		Geranium molle		*Fragaria viridis*	
		Poa pratensis		*Galium verum*	
		Ranunculus acris		*Linaria vulgaris*	
		Rapistrum rugosum		*Melilotus albus*	
		Vicia sepium		*Rorippa pyrenaica*	
		Vicia villosa		*Rumex thyrsiflorus*	
				Sambucus nigra	
				Sanguisorba minor	
				Sanguisorba officinalis	
				Securigera varia	
				Sedum acre	
	Limnic and terrestrial species	*Acer pseudoplatanus*	56.0	*Corylus avellana*	32.0
		Aristolochia clematitis		*Fraxinus excelsior*	
		Barbarea vulgaris		*Hypericum perforatum*	
		Calamagrostis epigejos		*Lathyrus pratensis*	
		Clematis vitalba		*Melilotus altissimus*	
		Galium mollugo		*Myosotis laxa*	
		Geranium pratense		*Potentilla anserina*	

		Hypericum maculatum *Lamium album* *Parthenocissus inserta* *Parthenocissus quinquefolia* *Populus trichocarpa* *Quercus robur* *Ranunculus repens* *Raphanus sativus* *Silene dioica* *Sisymbrium officinale* *Vicia cracca*		*Prunus spinosa*	
F	Limnic biotope species	*Epilobium parviflorum* *Glyceria maxima* *Lysimachia vulgaris* *Rorippa anceps* *Salix fragilis*	25.0	*Carex acuta*	6.0
	Terrestrial biotope species	*Bromus sterilis* *Carduus nutans* *Rorippa pyrenaica* *Stachys annua* *Tilia platyphyllos* *Trifolium pratense*	30.0	*Betula pendula* *Cornus sanguinea* *Geum urbanum* *Trifolium pratense* *Verbena officinalis* *Viburnum lantana* *Vicia angustifolia* *Vicia villosa*	50.0
	Limnic and terrestrial species	*Acer campestre* *Carex hirta* *Cerastium glomeratum* *Cirsium oleraceum* *Heracleum sphondylium* *Juncus conglomeratus*	45.0	*Acer pseudoplatanus* *Deschampsia cespitosa* *Epilobium ciliatum* *Glechoma hederacea* *Phragmites australis* *Poa trivialis*	44.0

		Potentilla anserina *Salix eleagnos* *Ulmus minor*		*Ribes rubrum*	
U	Limnic biotope species	*Achillea ptarmica* *Impatiens glandulifera* *Thalictrum flavum*	31.0	*Scrophularia umbrosa* *Rumex aquaticus* *Rorippa anceps* *Veronica maritima* *Rorippa amphibia* *Glyceria maxima* *Valeriana procurrens* *Veronica catenata*	28.0
	Terrestrial biotope species	*Agrimonia eupatoria* *Centaurea nigrescens* *Cirsium tuberosum* *Rumex acetosella* *Sambucus nigra*	31.0	*Silene vulgaris* *Juncus effusus* *Lolium perenne* *Medicago falcata* *Arctium minus* *Capsella bursa-pastoris* *Daucus carota* *Lapsana communis* *Mentha spicata*	31.0
	Limnic and terrestrial species	*Atriplex patula* *Persicaria hydropiper* *Erysimum cuspidatum* *Salix rosmarinifolia* *Viola hirta*	38.0	*Acer negundo* *Cirsium vulgare* *Festuca gigantea* *Melilotus officinalis* *Mentha longifolia* *Rosa multiflora* *Rumex conglomeratus* *Rumex sanguineus* *Salix caesia*	41.0

					Taraxacum sect. Ruderalia *Trifolium dubium* *Ulmus minor*	

Table A2.11 - Site-associated species and their classification as C-, CR-, CS-, CSR-, R- and S-strategist for each bank type (riprap (R), front-fixed (F), unfortified (U)) and waterway that were used in the trait analysis as well as the percentage of the classification as part of the whole group. C- and CR-strategists are shown with their occurrence in each vegetation layer (tree, shrub, herb, grass). For species named as "Others" no characteristic values were available, thus statistical consideration was not possible.

Bank type	Classification	Vegetation layer	Main River	Percentage	Danube River	Percentage
R	C-Strategists	Tree	*Acer pseudoplatanus* *Quercus robur* *Salix purpurea*	10.0	*Fraxinus excelsior*	3.6
		Shrub	*Parthenocissus inserta*	3.3	*Corylus avellana* *Prunus spinosa* *Sambucus nigra*	10.7
		Herb	*Geranium pratense* *Ranunculus acris* *Galium album* *Vicia cracca* *Vicia sepium* *Anthriscus sylvestris* *Clematis vitalba* *Aristolochia clematitis* *Silene dioica*	30.0	*Echinops sphaerocephalus* *Hypericum perforatum* *Lathyrus pratensis* *Rumex thyrsiflorus* *Securigera varia* *Solanum dulcamara*	21.4
		Grass	*Festuca pratensis* *Bromus inermis* *Calamagrostis epigejos* *Poa pratensis*	13.3	*Elymus caninus* *Festuca rubra*	7.1
	CR-Strategists	Tree	-	0	-	0
		Shrub	-	0	-	0

		Herb	*Barbarea vulgaris* *Rapistrum rugosum* *Sisymbrium officinale* *Vicia villosa*	13.3	*Melilotus albus* *Melilotus altissimus*	7.1
		Grass	-	0	-	0
	CS-Strategists		*Iris pseudacorus* *Dactylis polygama* *Galium verum* *Salix viminalis* *Scrophularia auriculata*	16.7	*Angelica archangelica* *Achillea ptarmica* *Galium verum* *Sanguisorba officinalis*	14.3
	RS-Strategists		-	0	-	0
	CSR-Strategists		*Lamium album* *Hypericum maculatum* *Ranunculus repens*	10.0	*Myosotis laxa* *Agrostis vinealis* *Filipendula vulgaris* *Fragaria viridis* *Linaria vulgaris* *Potentilla anserina* *Rorippa pyrenaica* *Sanguisorba minor*	28.6
	R-Strategists		*Geranium molle*	3.3	*Bromus tectorum*	3.6
	S-Strategists		-	0	*Sedum acre*	3.6
	Other		*Raphanus sativus* *Parthenocissus quinquefolia* *Populus trichocarpa*	-	-	-
F	C-Strategists	Tree	*Acer campestre* *Salix eleagnos* *Salix fragilis* *Tilia platyphyllos* *Ulmus minor*	25.0	*Acer pseudoplatanus* *Betula pendula*	12.5

		Shrub	-	0	*Cornus sanguinea* *Ribes rubrum*	12.5
		Herb	*Cirsium oleraceum* *Heracleum sphondylium* *Trifolium pratense*	15.0	*Epilobium ciliatum* *Trifolium pratense*	12.5
		Grass	*Carex hirta* *Juncus conglomeratus*	10.0	*Deschampsia cespitosa*	6.3
		Shrub	-	0	-	0
		Herb	*Carduus nutans*	5.0	*Verbena officinalis* *Vicia angustifolia* *Vicia villosa*	18.8
		Grass	*Bromus sterilis*	5.0	-	0
	CS-Strategists		*Epilobium parviflorum* *Glyceria maxima* *Lysimachia vulgaris* *Rorippa anceps*	20.0	*Carex acuta* *Phragmites australis* *Viburnum lantana*	18.8
	RS-Strategists		-	0	-	0
	CSR-Strategists		*Potentilla anserina* *Rorippa pyrenaica*	10.0	*Geum urbanum* *Glechoma hederacea* *Poa trivialis*	18.8
	R-Strategists		*Cerastium glomeratum* *Stachys annua*	10.0	-	0
	S-Strategists		-	0	-	0
	Other		-	-	-	-
U	C-Strategists	Tree	-	0	*Acer negundo* *Ulmus minor*	7.4
		Shrub	*Sambucus nigra*	8.3	-	0
		Herb	*Agrimonia eupatoria* *Centaurea nigrescens*	33.3	*Arctium minus* *Mentha longifolia*	18.5

		Cirsium tuberosum *Thalictrum flavum*		*Mentha spicata* *Rumex conglomeratus* *Valeriana procurrens*	
	Grass	-	0	*Juncus effusus* *Lolium perenne*	7.4
CR-Strategists	Tree	-	0	-	0
	Shrub	-	0	-	0
	Herb	*Atriplex patula* *Impatiens glandulifera* *Persicaria hydropiper*	25.0	*Cirsium vulgare* *Daucus carota* *Lapsana communis* *Melilotus officinalis*	14.8
	Grass	-	0	-	0
CS-Strategists		*Achillea ptarmica* *Salix rosmarinifolia*	16.7	*Festuca gigantea* *Glyceria maxima* *Medicago falcata* *Rorippa amphibia* *Rorippa anceps* *Rumex aquaticus* *Rumex sanguineus* *Scrophularia umbrosa* *Veronica catenata* *Veronica maritima*	37.0
RS-Strategists		-	0		0
CSR-Strategists		*Rumex acetosella* *Viola hirta*	16.7	*Silene vulgaris* *Taraxacum sect. Ruderalia*	7.4
R-Strategists		-	0	*Capsella bursa-pastoris* *Trifolium dubium*	7.4
S-Strategists		-	0	-	0
Other		*Erysimum cuspidatum*	-	*Rosa multiflora*	-

	Salix caesia

Table A2.12 - Kilometers of each study site and the surrounding dams for each waterway.

Waterway	Study site	km	Present dams	km
Main	Markheidenfeld	180.0 – 182.0	Lengfurt	174.5
			Rothenfels	185.8
	Gemünden a. M.	211.1 – 212.7	Steinbach	200.6
			Harrbach	219.4
	Kitzingen	287.4 – 288.7	Kitzingen	283.9
	Obereisenheim	313.5 – 315.5	Gerlachshausen	300.5
			Wipfeld	316.2
Danube	Pfatter	2351.1 – 2348.0		
	Irling	2345.7 – 2343.7	Geisling	2354.2
	Aholfing	2343.0 – 2341.5	Straubing	2324.1
	Obermotzing	2338.0 – 2336.0		

Chapter 3

Riparian plant species composition alternates between species from standing and flowing water bodies – Results of field studies upstream and downstream of weirs along the German rivers Lahn and Fulda

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Abstract

Regulation measures like the installation of weirs led to distinct shifts in riparian plant communities and to a decline of typical riparian plant species occurring along the river shoreline, which is naturally poor in woody plants. These regulation measures include also run-of-river impoundments or weirs that cause distinct differences in hydrodynamic conditions in their direct proximity upstream and downstream. In the course of the year, the downstream reaches are exposed to significantly higher water level fluctuations than upstream. Thus, these reaches are assumed to provide also suitable habitat for riparian plant species of habitats being exposed to frequent disturbance by alternating water levels.

We investigated the riparian vegetation in direct proximity upstream and downstream of nine weirs along the two regulated rivers Lahn and Fulda. Sampling was conducted in the transition zone from water to land directly above the actual water level during the summers 2016 and 2017. Differences in species composition were analyzed by means of NMS and indicator species analysis. Results of the indicator species analysis were used for further analyses regarding species´ functional traits and species´ habitat origin.

A grouping of the relevés in accordance to the weir reach, dissimilarities in site conditions, significant indicator species for each weir reach and common indicator species upstream along both rivers point towards differences in species composition upstream and downstream. Due to rather constant water levels, upstream species composition consisted mainly of perennial species from reeds of still waters, swamp and alluvial forests and terrestrial habitats that were mainly competitors. By contrast, species from reeds of flowing waters, flooded meadows and grasslands and typical riparian plant communities (*Bidention tripartitae*, *Chenopodion rubri*) occurred more frequently downstream. Species downstream exhibited also less competitive power and short life cycles as a result of higher water level fluctuations.

Upstream and downstream species composition clearly reflect the observed hydrodynamic conditions, restricting continuity to the area within two weirs. This distinctly differs from natural conditions, which leads to the establishment of novel riparian plant communities. As downstream reaches in direct proximity to weirs are related to higher water level fluctuations in the course of the year, these areas are of essential meaning as refuge for typical riparian species. Against this background, we recommend to decrease bank steepness downstream to increase the effect of water level fluctuations, which would lead to the establishment of suitable habitats for typical riparian plant species.

3.1 Introduction

Riparian plant communities provide substantial environmental functions (NAIMAN ET AL., 1993) and harbor a wide range of specialized species that evolved over a long time (DÉCAMPS, 2011) as they are naturally governed by disturbances by alternating water levels that vary in space and time (WARD, 1998). As a result, these areas are characterized by a zonation of differing plant communities being located in near proximity to each other and thus are closely interlinked (ELLENBERG AND LEUSCHNER, 2010).

Regulation measures like bank steepening, river straightening and the installation of impoundments resulted in enormous alterations of the natural dynamic disturbance regime and discontinuities in the riparian corridor (PAUL AND MEYER, 2001; BUNN AND ARTHINGTON, 2002). As a consequence, the space for the development of the zonation with riparian plant communities was reduced over time, leading to the establishment of novel assemblies of riparian plant communities (MERRITT AND WOHL, 2006). This is especially true for the shoreline which is nowadays naturally poor in woody plants, mainly consisting of species from nitrophilous tall herb communities (*Galio-Urticenea*) with high nutrient and moisture demands that are less tolerant against flooding (OBERDORFER, 1993). By contrast, space availability for floodplain biotope types is strongly reduced, which require frequent water level fluctuations. While reeds of flowing waters and flooded meadows and grasslands react less sensitively towards alterations of the natural disturbance regime, riparian plant communities of the *Bidention tripartitae* and *Chenopodion rubri* rely on water level fluctuations and therefore are in decline (FEDERAL AGENCY FOR NATURE CONSERVATION, 2011). Species from these biotope types are capable to pass their entire life cycle during low water level phases in the summer time, thus exhibiting high seed production, short life cycles but low competitive power (ELLENBERG AND LEUSCHNER, 2010; OBERDORFER, 1993). Due to the installation of embankments and bank steepening, these biotope types are classified as strongly endangered and meanwhile rare in Germany (FINCK ET AL., 2017). Similar tendencies apply also for other European rivers, as a particularly high amount of the global regulation measures was performed along European rivers (NILSSON ET AL., 2005). Therefore, these habitats are protected by the EU Habitats Directive (Council Directive 92/43/EEC, habitat type 3270: rivers with muddy banks with *Chenopodion rubri* p.p. and *Bidention* vegetation p.p.), which is applicable to give orientation for the definition of targets in planning of restoration measures.

Impoundments rank among the most implemented regulation measures, since at least two-thirds of all running waters around the world were impounded (PETTS, 1984) for irrigation, navigation, flood control and hydropower purposes (BELLMORE ET AL., 2017; NILSSON AND BERGGREN, 2000; SHAFROTH ET AL., 2002). The installation of impoundments along two-thirds of the German Federal Waterway network was mainly performed for the facilitation of shipping traffic

(STAMM, 2006). Although impoundments in rivers have a long tradition in running waters (NEUBECK, 2014), the evoking ecological consequences only gained enhanced attention through the adoption of the European Water Framework Directive, which aims to achieve a good ecological potential along regulated rivers (THE EUROPEAN PARLIAMENT, 2000a).

In comparison to free-flowing rivers, the installation of impoundments led to severely altered hydrodynamic conditions, which is disclosed by a decline in flooding frequency and intensity (POFF ET AL., 2007; POFF & ZIMMERMAN, 2010; JANSSON ET AL., 2000). Depending on the type of impoundment, flooding seasonality is weakened as water discharge is anthropogenically controlled (BUNN & ARTHINGTON, 2002). The term *impoundment* refers to a broad range of construction methods like dams and run-of-river impoundments (hereafter referred to as weirs) that differ in size and extent. One extreme is the Three Gorges dam built in the large river Yangtze in China (NEW & XIE, 2008), where the dam distinctly changes the total landscape and water level fluctuations are strongly dependent from the dam management as water is mainly stored in the reservoir below the dam crest (CSIKI & RHOADS, 2010; BEJARANO ET AL., 2018). By contrast, smaller impoundments like weirs are more common along smaller rivers like the Lahn and Fulda in Hesse, where they occur in sequences. Compared to dams, water in rivers being regulated by weirs runs permanently over the crest during the whole year, but maintaining at least some flood seasonality along the downstream reaches (CSIKI & RHOADS, 2010).

Nevertheless, weir installation leads to discontinuities in the river´s natural flow regime, which is displayed by distinct differences in water level fluctuation and flow velocity in direct proximity upstream and downstream of weirs. Substantial reductions in flow velocity upstream are induced by lateral extension of the flowing channel in the direct weir area (JUNGWIRTH ET AL., 2006; JANSSON ET AL., 2000), leading to nearly constant water levels in the river channel and an increasing riverbed depth directed to the weir (STATE OFFICE FOR WATER MANAGEMENT OF RHINELAND-PALATINATE, 1997). Due to low water level fluctuations, the transition zone from aquatic to terrestrial areas is substantially smaller compared to free-flowing rivers (ANDERSSON ET AL., 2000). By contrast, transition zone downstream is wider, as hydrological conditions are characterized by stronger water level fluctuations and increased exposures to seasonal fluctuations (STATE OFFICE FOR WATER MANAGEMENT OF RHINELAND-PALATINATE, 1997). Furthermore, higher flow velocities than upstream are prevalent (BUSCH, 2006). The erosive power of the weir-passing water results in increasing river bed degradation leading to gradual lowering of the corresponding groundwater level and thus a successive reduction of the active floodplain (NILSSON & BERGGREN, 2000; STAMM, 2006). Thus, the riverbed in direct proximity downstream of each weir is reinforced technically.

Riparian vegetation is very suitable to display the prevalent environmental conditions along rivers, thus weir-induced hydrodynamic differences are expected to be well represented (NILSSON & BERGGREN, 2000). So far, there are evidences that impoundments obstruct hydrochorous seed dispersal (ANDERSSON ET AL., 2000; MERRITT & WOHL, 2006), alter riparian zonation (NEW & XIE, 2008), decrease species plant diversity (DYNESIUS ET AL., 2004) and lead to alterations in plant species composition (MERRITT & COOPER, 2000; NILSSON & JANSSON, 1995) and thus in functional diversity (NEW & XIE, 2008). Nevertheless, studies on weir impact on riparian vegetation are still underrepresented as most studies focus on impacts of dams on riparian vegetation (MALLIK & RICHARDSON, 2009; ELDERD, 2003) and comparisons of riparian vegetation along free-flowing and impounded rivers (JANSSON ET AL., 2000; NILSSON & JANSSON, 1995). Actually, little is known in which way upstream and downstream riparian vegetation is affected by weirs and what options for successful restoration measures along impounded rivers exist.

Therefore, we studied the riparian vegetation above the mean water level in direct proximity of nine weirs along the rivers Lahn and Fulda to disentangle the effects of weir-induced differences in hydrodynamic conditions for riparian vegetation. Our investigation focuses on the following questions:

- Are there differences in species composition between upstream and downstream riparian vegetation?
- How do species react to upstream and downstream site conditions in terms of life strategy and longevity?
- Do impounded rivers provide remnant habitats for species being related to hydrodynamic habitats?

  What can be concluded for the restoration management along impounded rivers?

3.2 Methods

3.2.1 Study areas

The study areas are located in Central Germany and cover the stretches of the rivers Lahn (km 3.6 to 97.7, 153 m a.s.l., Dorlar to 100 m a.s.l., Scheidt) and Fulda (km 60.0 to 102.4, 180 m a.s.l., Neumorschen to 146 m a.s.l., Wilhelmshausen) (Fig. 3.1).

Both rivers are modified by weirs, which were installed during the Middle Ages for mills and hammer mills (NEUBECK, 2014; STATE OFFICE FOR WATER MANAGEMENT OF RHINELAND-PALATINATE, 1997). Regulation measures in the past included also bank stabilization with ripraps, riverbed deepening and the removal of gravel banks and large stones in the riverbed (FEDERAL WATERWAYS AND SHIPPING ADMINISTRATION, 2008; NEUBECK, 2014). Maintenance measures are limited to mowing of lockages, waterway signs and water level monitoring stations, the removal of flow barriers (trees, gravel banks) and improvement works of bank revetments (J. SCHMIDT, Federal Waterways and Shipping Administration, personal communication, January 31, 2017).

Beside a good accessibility in the field, we defined a low population density in adjacent areas to exclude potential related effects as far as possible and at least one kilometer distance to the next weir to avoid mutual influence of backwaters as requirements for the weir selection.

We recorded the vegetation of six study sites at the Lahn (Dorlar, Naunheim, Niederbiel/Oberbiel, Löhnberg, Fürfurt, Scheidt) and three study sites at the Fulda (Neumorschen, Melsungen, Wilhelmshausen), resulting in nine study sites in total. The Lahn study sites Dorlar, Naunheim and Niederbiel/Oberbiel are located in the biogeographic region of the eastern Hessian mountainous and sink countries, whereas Löhnberg, Fürfurt and Scheidt belong to the river Lahn valley of Giessen and Koblenz. The Fulda study sites Neumorschen and Melsungen are situated in the East Hessian Highlands, while Wilhelmshausen is part of the Weser-Leine-Highlands (KLAUSING, 1988).

Due to a higher weir density along the Lahn, the majority of our study sites are located along the Lahn. Since the weirs of Niederbiel and Oberbiel were separated by a weir channel of too short distance to each other (1000 m) for our study requirements, we sampled all upstream relevés upstream of the weir in Oberbiel and all downstream relevés downstream of the weir in Niederbiel.

According to NILSSON & BERGGREN (2000) rivers are characterized by an individual flow regime, geology, topography, climate and thus vegetation. Thus, comparing vegetation between rivers is challenging. However, as we aim to derive general findings on the impact of weirs on riparian plant vegetation, we attached importance on at least similarities in the selection of study rivers. This applies to climatic conditions, the river´s flow regime (detailed information in table 3.1), regulation measures and maintenance intensity as these factors are verified to affect riparian plant species composition (NILSSON & BERGGREN, 2000; HARVOLK ET AL., 2015; WOLLNY ET AL., 2019). As both rivers prove differences in their regional species composition, we studied each river dataset separately and compared our results with respect to consistency in trends between both rivers. This provides the opportunity to reveal differences in species´ response that are related to the design of weirs.

Table 3.1 - Specification of local site conditions at study sites along the Lahn and Fulda regarding general (climate, geology, soil types, hydrological properties) and investigated site conditions (edaphic conditions, bank inclination). Upstream and downstream reaches are further specified respecting mean water level, mean water level fluctuation, edaphic conditions and bank inclination (mean ± standard deviation). Asterisks mark the significance level (*p < 0.05; **p < 0.01; ***p < 0.001) detected by a Wilcoxon rank sum-test in R 3.4.4. Similar letters indicate homogenous groups. Data on water level and water level fluctuation display the yearly mean values. These data were provided for each relevé and were retrieved from FLYS 3.2.1 (German Federal Institute of Hydrology 2018), a software that is based on long-term hydrological data and high-resolution digital ground models. References: Climate (Lahn): German Meteorological Service (2018), climate (Fulda): Hessian State Office for Environment and Geology (2013c); geological understorey: Hessian State Office for Environment and Geology (2013b); dominating soil types: Hessian State Office for Environment and Geology (2013a); flow regime: Koenzen (2005); mean water discharge (Lahn, water level monitoring station Kalkhofen; Fulda, water level monitoring station Bonaforth): Federal Waterways and Shipping Administration (2019).

			Lahn		**Fulda**	
		Specification	**Upstream (n=48)**	**Downstream (n=48)**	**Upstream (n=24)**	**Downstream (n=24)**
General site conditions	Climate	Mean annual temperature (°C)	9.6		8-9	
		Mean annual precipitation (mm)	666		500	
	Geological understorey	-	Holocene alluvial sediments		Holocene alluvial sediments	
	Dominating soil types	-	Fluvisols, Cambisols		Fluvisols, Cambisols	
	Hydrological properties	Flow regime	Pluvial		Pluvial	
		Mean water discharge 1986-2015 (m^3 s^{-1})	45.1 ± 26.9		62.8 ± 26.7	
		Mean water discharge 2016 (m^3 s^{-1})	37.2 ± 32.1		54.6 ± 35.4	
		Mean water discharge 2017 (m^3 s^{-1})	40.6 ± 32.6		51.6 ± 34.8	
		Mean water level (cm)	133.1 ± 19.0	130.7 ± 19.5	145.7 ± 17.3	143.5 ± 17.0
		Mean water level fluctuation (m)***	1.6 ± 0.3 (a)	3.4 ± 1.2 (b)	1.2 ± 0.2 (A)	2.7 ± 0.2 (B)
Investigated site conditions	Edaphic properties	P_2O_5 (g kg^{-1})	154.1 ± 52.5	162.7 ± 57.1	131.1 ± 63.9	144.8 ± 37.1
		K_2O (g kg^{-1})	115.1 ± 67.2	104.7 ± 50.7	96.7 ± 80.4	69.5 ± 26.9
		N_{total} (%)***	0.4 ± 0.1	0.4 ± 0.1	0.3 ± 0.1 (A)	0.2 ± 0.1 (b)
		C_{total} (%)**	4.6 ± 1.2	4.5 ± 1.6	3.8 ± 1.8 (A)	2.7 ± 0.8 (B)
	Bank inclination (%)***	-	18.2 ± 16.2 (a)	28.0 ± 18.5 (b)	13.2 ± 6.5 (A)	43.0 ± 29.0 (B)

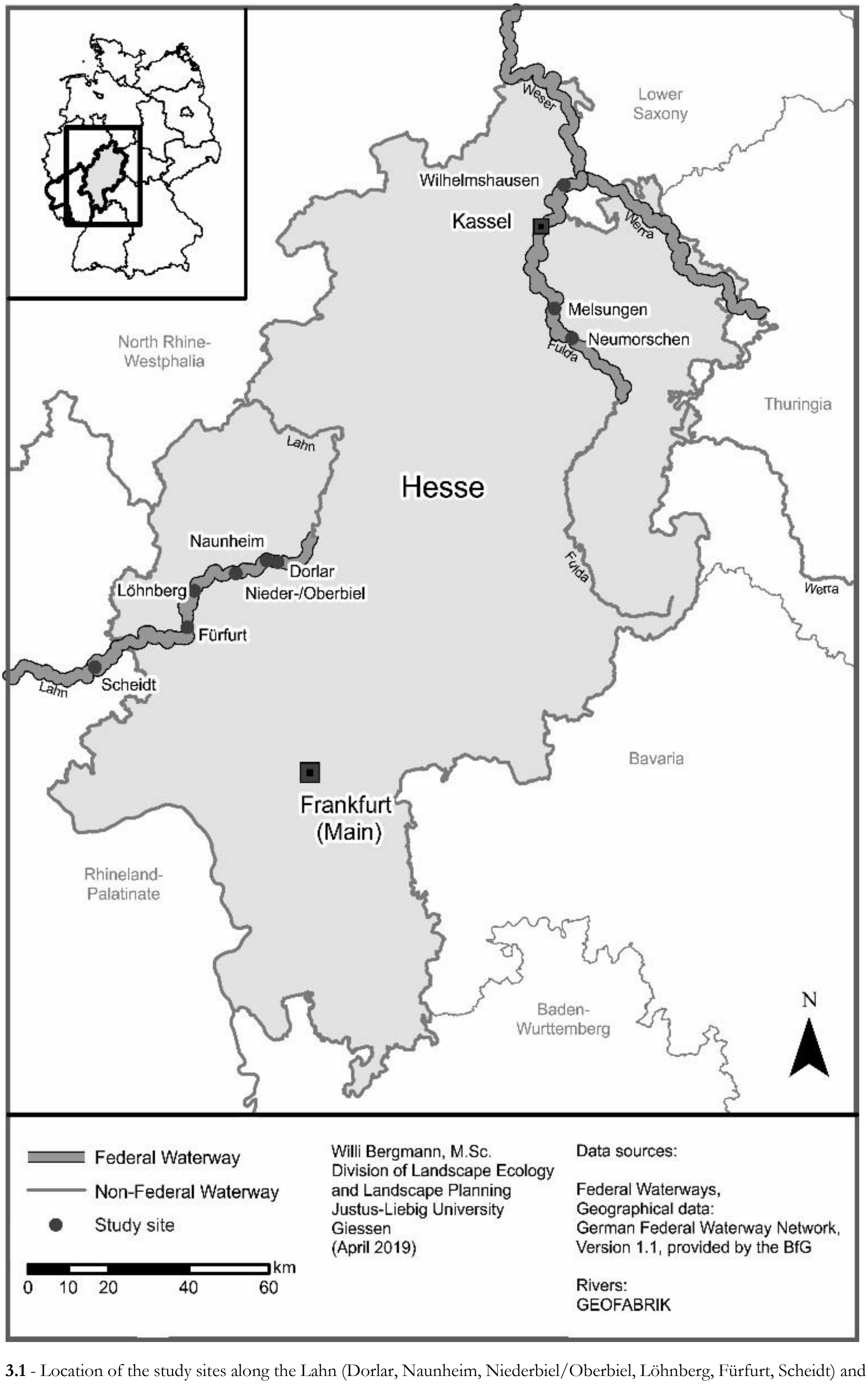

Fig. 3.1 - Location of the study sites along the Lahn (Dorlar, Naunheim, Niederbiel/Oberbiel, Löhnberg, Fürfurt, Scheidt) and the Fulda (Neumorschen, Melsungen, Wilhelmshausen).

3.2.2 Study design, vegetation and environmental variables

We recorded the vegetation on the right- and on the left-hand bank upstream and downstream from each weir. We used distances of 200 m, 400 m, 800 m and 1000 m to test also for differences in species composition with increasing distance to the weir. For security reasons, data collection upstream and downstream started at 200 m distance to the weir. We collected vegetation data in 16 relevés for each weir, resulting in 144 relevés in total (Fig. 3.2). For an illustration of the site conditions at the weir in Fürfurt, we refer to Figs. A3.1, A3.2 and A3.3 in the Supporting information.

Each relevé was sampled in the riparian transition zone directly above the actual water level in long and narrow strips of 2 m width and 10 m length, as recommended by DYNESIUS ET AL. (2004), during the summers of 2016 and 2017. Data on weather conditions in 2016 and 2017 compared to the long-term weather conditions (1986-2015) are provided in Fig. 3.3, whereas sampling months and years are listed in Table A3.1. Sampling was carried out once for each relevé. Species abundances were estimated with the modified Braun-Blanquet numerical scale (VAN DER MAAREL, 1979). Plants were identified according to the nomenclature of JÄGER (2013). The herb layer was subdivided into grass and herb fraction for further analyses regarding potential differences in upstream and downstream species composition.

In order to receive information about the prevalent local site conditions, each relevé was supplemented by mixed soil samples for chemical analyses. Soil sampling was performed with a *Puerckhauer*-boring rod (ø 2.5 cm) and comprised three soil cores in the topsoil (0-10 cm) regularly distributed across each relevé. As preparation for further analyses, every soil sample was dried and sieved (2 mm). Calcium-acetate-lactate (CAL) extraction (SCHÜLLER, 1969) was used for the detection of plant available phosphorus and potassium contents, whereas contents of total carbon and nitrogen were determined by an elementary analyzer (Automatic Elemental Analyzer EA/NA 1110, TermoQuest Italia S.p.A.).

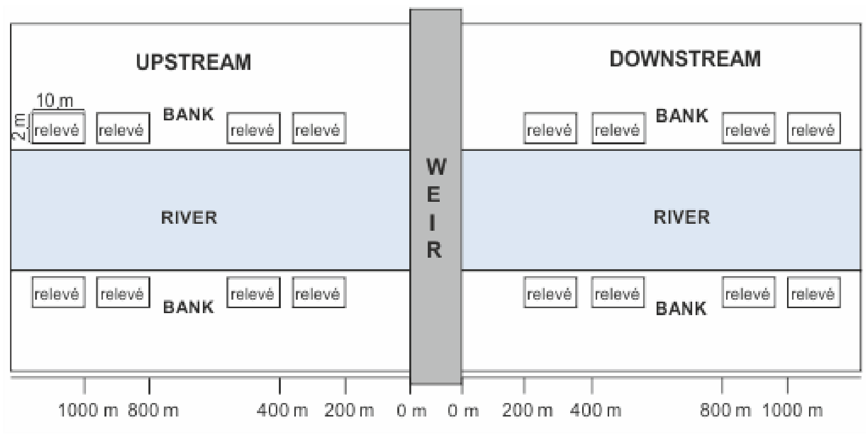

Fig. 3.2 - Sampling design for data collection in the field.

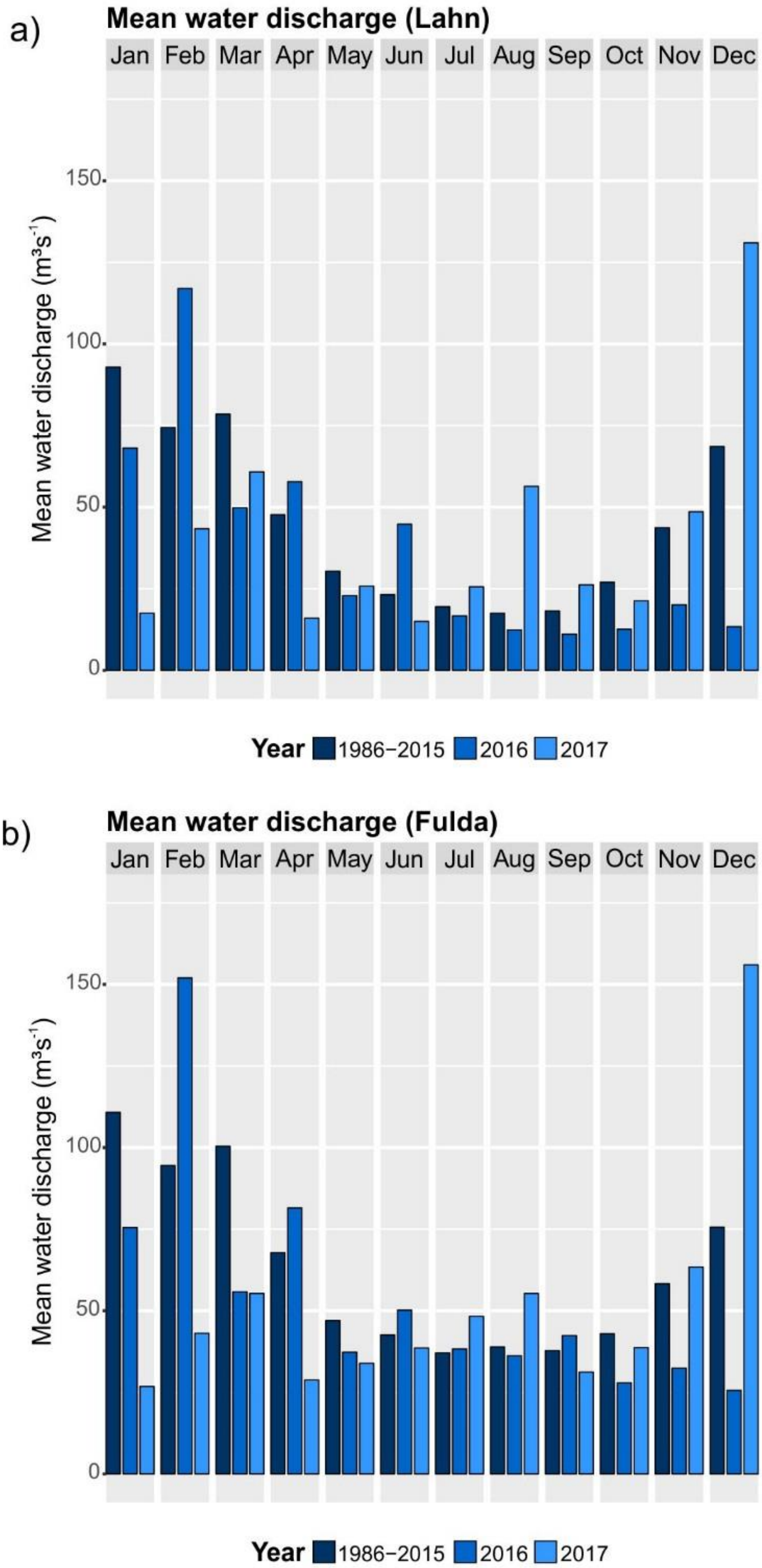

Fig. 3.3 - Long-term mean water discharges (1986-2015) and mean water discharges for the sampling years 2016 and 2017 for each river (a) Lahn: water level monitoring station Kalkhofen; b) Fulda: water level monitoring station Bonaforth) as a proxy for the weather conditions during the vegetation sampling provided by the FEDERAL WATERWAYS AND SHIPPING ADMINISTRATION (2019).

3.2.3 Statistical analyses

Differences in species composition between upstream and downstream reaches (*reach* is defined as the river stretch one kilometer upstream and downstream from weirs, where weir impact on hydrodynamic conditions is expected to be the largest (J. SCHMIDT, Federal Waterways and Shipping Administration, personal communication, January 31, 2017)) of the sampled weirs were analyzed by non-metric multidimensional scaling (NMS) based on Sørensen distances (Bray-Curtis distance). Prior to the analysis, we adjusted 200 iterations, three dimensions and a random starting configuration as analysis criteria. For an adequate representation of rare species in the dataset, percentage values of species abundances were transformed via square root transformation. An overview of the environmental variables used for NMS is provided in Table 3.2. Ordination was carried out with PC-ORD 5.33 (MCCUNE & MEFFORD, 2006).

Significant indicator species for each weir reach were determined by an indicator species analysis (DUFRÊNE & LEGENDRE, 1997). Decisive characteristics for significant indicator species were an indicator value (IV) >25 and a p-value <0.05 (DUFRÊNE & LEGENDRE, 1997). We used the R-package *indicspecies* (CÁCERES & LEGENDRE, 2009) for our indicator species analysis in R 3.4.4 (R DEVELOPMENT CORE TEAM, 2015).

Statistical differences in soil chemical analyses, mean water level fluctuation and bank inclination (Table 3.1) between upstream and downstream weir reaches were tested with a Wilcoxon rank-sum test in R 3.4.4 (R DEVELOPMENT CORE TEAM, 2015) for reasons of inhomogenous variances and for lack of normally distributed data.

Table 3.2 - Categories, environmental variables, their abbreviations and units used for NMS.

Category	Variable	Abbreviation	Unit
Topography	Altitude	Altitude	m
	Inclination banks	Inclin	%
Vegetation	Cover tree layer	Cov_tree	%
	Cover shrub layer	Cov_shrub	%
	Cover herb layer	Cov_herbs	%
	Cover grass layer	Cov_grass	%
	Cover litter layer	Cov_litter	%
	Cover open soil	Cov_soil	%
Species diversity	Richness	Richness	Unitless
	Shannon index	Shannon	Unitless
	Evenness	Evenness	Unitless
Local site conditions	Water level fluctuation	Water level fluctuation	m
	Mean Ellenberg indicator value (light)	EIV Light	Unitless
	Mean Ellenberg indicator value (moisture)	EIV Moisture	Unitless
	Mean Ellenberg indicator value (nutrient)	EIV Nutrient	Unitless
	Phosphorous content soil	P_2O_5	g kg $^{-1}$
	Potassium content soil	K_2O	g kg $^{-1}$
	Total carbon content soil	Ctot	%
	Total nitrogen content soil	Ntot	%

3.2.4 Analysis of ecological and functional groups

Indicator species analysis detected indicator species for upstream and downstream reaches that were either significant or not significant. While significant indicator species are characterized by both higher relative abundances and relative frequencies along either upstream or downstream reaches, not significant species at least show higher relative frequencies along either upstream or along downstream reaches (DUFRÊNE & LEGENDRE, 1997). Thus, these species show preferences to one reach and are assumed to have improved adaptations to the site conditions prevalent along the respective reach. Although these groups of reach-associated species are not necessarily equal in species numbers, they are of high relevance for the ecological assessment of the prevalent patterns between upstream and downstream reaches. Due to regulation measures, rivers nowadays are characterized by a uniform character which also led to uniform vegetation patterns (WALSH ET AL., 2005). Thus, displaying differences in vegetation patterns due to differences (which are limited due to regulation) in hydroregime is challenging. Stand-forming species like *Urtica dioica* or *Impatiens glandulifera* are expected to mask differences in species composition as species with lower abundances and frequencies remain underrepresented. To circumvent this, we excluded stand-forming species from our analysis of ecological and functional species traits. These species occur with high abundances and frequencies in our datasets (chapter 3.1) but do not statistically show preferences to either upstream or downstream reaches (Lahn: Table A3.4, Fulda: Table A3.6), therefore bearing less explanation value. The exclusion of these species from our analysis enables us to conduct a more detailed analysis regarding differences in species composition and thus in species´ ecological and functional traits between upstream and downstream reaches.

We used BiolFlor (KÜHN ET AL., 2004) as data source for species´ strategy types and species´ longevity. The csr-concept after GRIME (1979) was used to describe species´ life strategy in response to the prevalent hydrodynamic conditions upstream and downstream.

To test for further differences in species composition, species occurrences upstream and downstream were analyzed by their habitat binding. Data on species´ habitat binding were retrieved from FloraWeb, a database that provides a diverse pool of information on wild plant species in Germany (e.g. taxonomy, status, habitat binding) and which is provided by the German Federal Agency for Nature Conservation. We retrieved all available information on habitat binding (classified as *major occurrences*, *main occurrences* and *minor occurrences*) for each species which were listed under the heading "Formation" (KORNECK ET AL., 1998). As information on species´ habitat binding being categorized as *major occurrences* were hardly available, we focused our subsequent analyses on information being categorized as *main occurrences*. This category reflects regular occurrences of species in the respective habitat (FEDERAL AGENCY FOR NATURE CONSERVATION, 2019). We focused our analyses on all available habitats that were related to floodplains: Swamp and alluvial forests (*Alnion-glutinosae, Alno-Ulmion*) as habitat reflecting low water flow velocities, nitrophilous tall herb communities (*Galio-Urticenea*) due to high amounts of these species in riparian plant communities along regulated rivers, flooded meadows and grasslands on trampled ground (*Agrostietea stoloniferae, Plantaginetea majoris*) as habitats reflecting flooding and bur-marigold and orache communities (*Bidentetea;* which includes species both from the *Bidention tripartitae* and *Chenopodion rubri* alliances) as habitats diplaying water level fluctuations. Beyond floodplain-related habitats, we analyzed also species information on arable land and annual ruderal communities (*Chenopodietea*) as these habitats also represent recurring disturbance events.

3.3 Results

3.3.1 Species composition

In total, 175 species were recorded at the Lahn, whereas the total species number at the Fulda amounted to 125 species. The combined dataset consists of 198 species, of which 102 (51%) species occurred at both rivers. Along both rivers, the highest relative frequencies were observed for *Urtica dioica* (Lahn: 63%, Fulda: 98%), *Impatiens glandulifera* (Lahn: 57%, Fulda: 88%), *Calystegia sepium* (Lahn: 47%, Fulda: 79%) and *Galium aparine* (Lahn: 45%, Fulda: 79%). These species are typical for the nitrophilous tall herb communities of river banks. Significant differences in the mean species number were not detectable, but species richness tended to be higher upstream than downstream (Lahn upstream: 19.6 ± 8.3, Lahn downstream: 16.3 ± 6.4; Fulda upstream: 22.3 ± 6.4, Fulda downstream: 20.2 ± 5.7). There were no differences detectable between relevés nearer and further from the weir, neither upstream nor downstream. Hence, we differentiated solely between upstream and downstream reaches in our further analyses.

Separate NMS (Fig. 3.4) revealed a grouping of the relevés in accordance to the weir reach, which was clearer for the Fulda than for the Lahn vegetation data. Relevés located along the downstream reach were exposed to larger water level fluctuations and were characterized by species with higher moisture, light and nutrient demands (EIVs) (Table A3.2 for detailed information on correlations for environmental variables). Higher nutrient levels in the downstream reaches become also apparent by a stronger correlation of the soil phosphorous and nitrogen content at the Lahn (Fig. 3.4a). Soils at the relevés along the Fulda upstream reaches were characterized by a higher potassium content (Fig. 3.4b).

Despite a significantly higher bank inclination in the downstream weir reaches (Table 3.1), bank inclination played a minor role for the variation in the dataset in our ordination (Lahn: $r^2=0.069$ along axis 1; Fulda: $r^2=0.172$ along axis 2) compared to the factor water level fluctuation (Lahn: $r^2= 0.225$ along axis 1; Fulda: $r^2=0.234$ along axis 2).

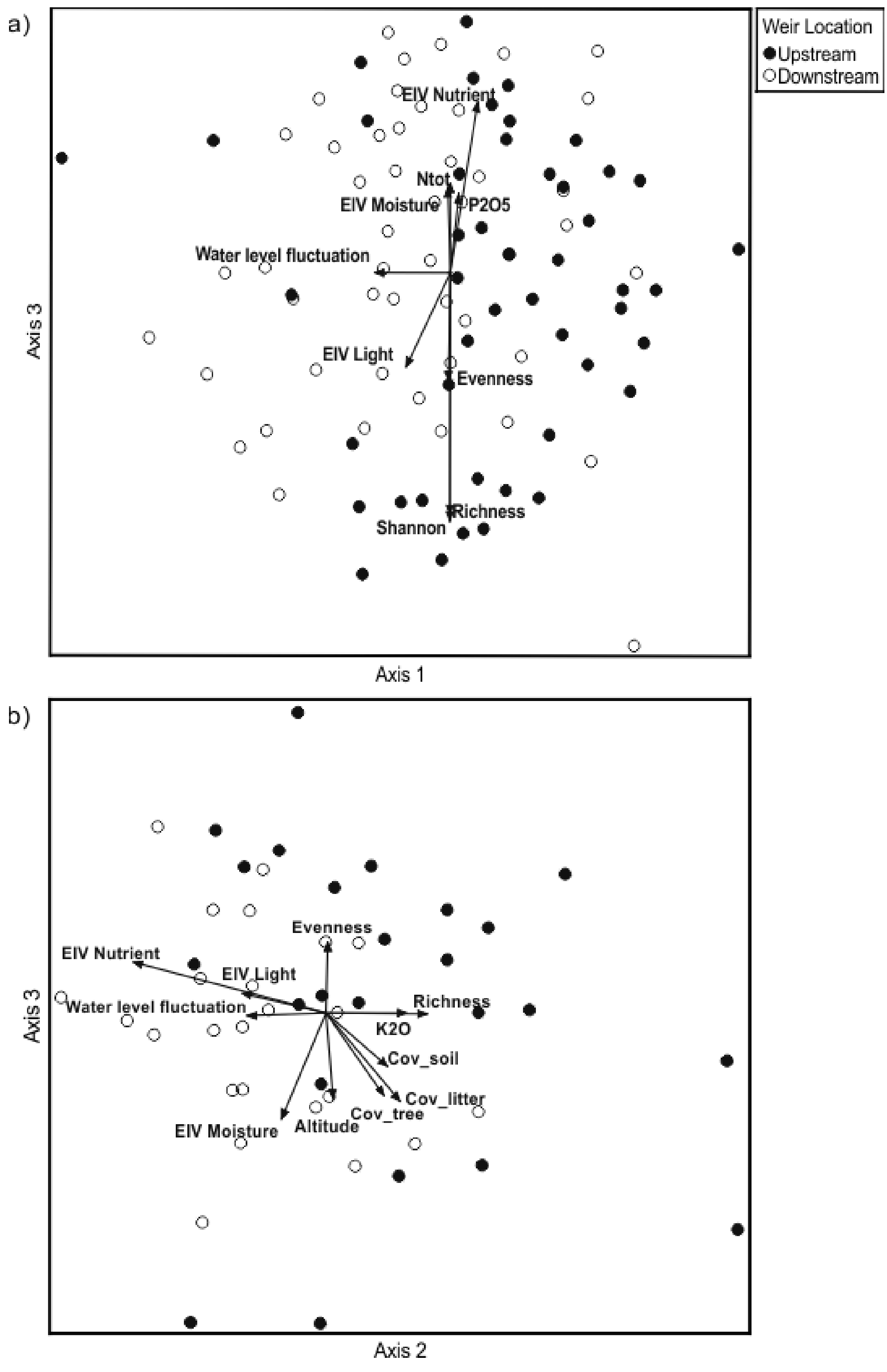

Fig. 3.4 - Final three-dimensional non-metric multidimensional scaling (NMS) plots based on Bray-Curtis dissimilarities displaying vegetation data of the rivers Lahn and Fulda. Every symbol refers to one relevé. Figure a) shows the Lahn ordination plot with a final stress of 20.34 and all environmental variables with $r^2>0.2$. Axis 3 ($r^2=0.340$), axis 1 ($r^2=0.174$) and axis 2 ($r^2=0.140$; not shown) constitute to a total variance explanation level of 65.4%. Figure b) displays the Fulda ordination plot with a final stress of 18.05 and all environmental variables with $r^2>0.2$. Total variance explanation level amounts to 75.5% and is explained by axis 2 ($r^2=0.339$), axis 3 ($r^2=0.241$) and axis 1 ($r^2=0.176$; not shown). Further details regarding the correlation levels of environmental variables are visible in Table A3.2.

Indicator species analysis (Table 3.3) revealed more significant indicator species for the upstream weir reaches than for the downstream ones at both rivers. *Filipendula ulmaria* was determined as common and highly significant indicator species for the upstream reaches along both rivers, whereas the downstream reaches had no indicator species in common. Upstream indicator species at the Lahn like *Stellaria graminea* and *Vicia sepium* showed mesic moisture demands, whereas upstream indicator species at the Fulda like *Lycopus europaeus* prefer higher moisture levels. Indicator species were mostly c-strategists, whereas r- or cr-strategists were absent in our dataset. No clear pattern was visible regarding species´ life strategy according to their occurrence upstream and downstream.

Table 3.3 - Significant indicator species for each reach and river with indicator value (IV), p-value, Ellenberg indicator value (EIV) for moisture and life strategy (Ellenberg et al., 1991). High EIV imply improved species adaptations to high moisture levels than species with lower EIV. Species´ life-strategies after Grime (1979): c=competitors, r=ruderal, s=stress tolerators and combinations thereof.

	Lahn					**Fulda**				
Reach	**Indicator species**	**IV**	**p-value**	**EIV moisture**	**Life strategy**	**Indicator species**	**IV**	**p-value**	**EIV moisture**	**Life strategy**
Upstream	*Filipendula ulmaria*	69.4	0.001***	8	c	*Filipendula ulmaria*	76.3	0.001***	8	c
	Aegopodium podagraria	62.5	0.002***	6	c	*Humulus lupulus*	56.8	0.012*	8	c
	Sambucus nigra	38.2	0.015*	5	c	*Phragmites australis*	63.2	0.02*	10	cs
	Stellaria graminea	35.4	0.026*	4	cs	*Lycopus europaeus*	59.3	0.022*	9	cs
	Heracleum sphondylium	34.0	0.029*	5	c	*Alopecurus pratensis*	55.4	0.037*	6	c
	Vicia sepium	35.4	0.03*	5	c					
	Rubus vulgaris	40.1	0.04*	5	c					
	Alnus glutinosa	48.1	0.041*	9	c					
Downstream	*Achillea ptarmica*	42.2	0.016*	8	cs	*Phalaris arundinacea*	89.3	0.001***	9	c
	Scrophularia nodosa	35.4	0.02*	6	cs	*Poa trivialis*	63.2	0.011*	7	csr
						Rumex obtusifolius	50.0	0.015*	6	c

Generally, banks along the Lahn and the Fulda were characterized by plant species mostly originating from nitrophilous tall herb communities, whereby the proportion downstream was higher than upstream (Fig. 3.5). Similarly, species from swamp and alluvial forests occurred also frequently along both rivers, but dominated along the upstream reaches, whereas species with main occurrences in arable land and annual ruderal communities tended to occur more frequently downstream. Patterns of species from flooded meadows and grasslands on trampled ground were contradictory. Species with origin in bur-marigold and orache bank communities were absent along the Fulda (Fig. 3.5b) and along the upstream reaches of the Lahn (Fig. 3.5a).

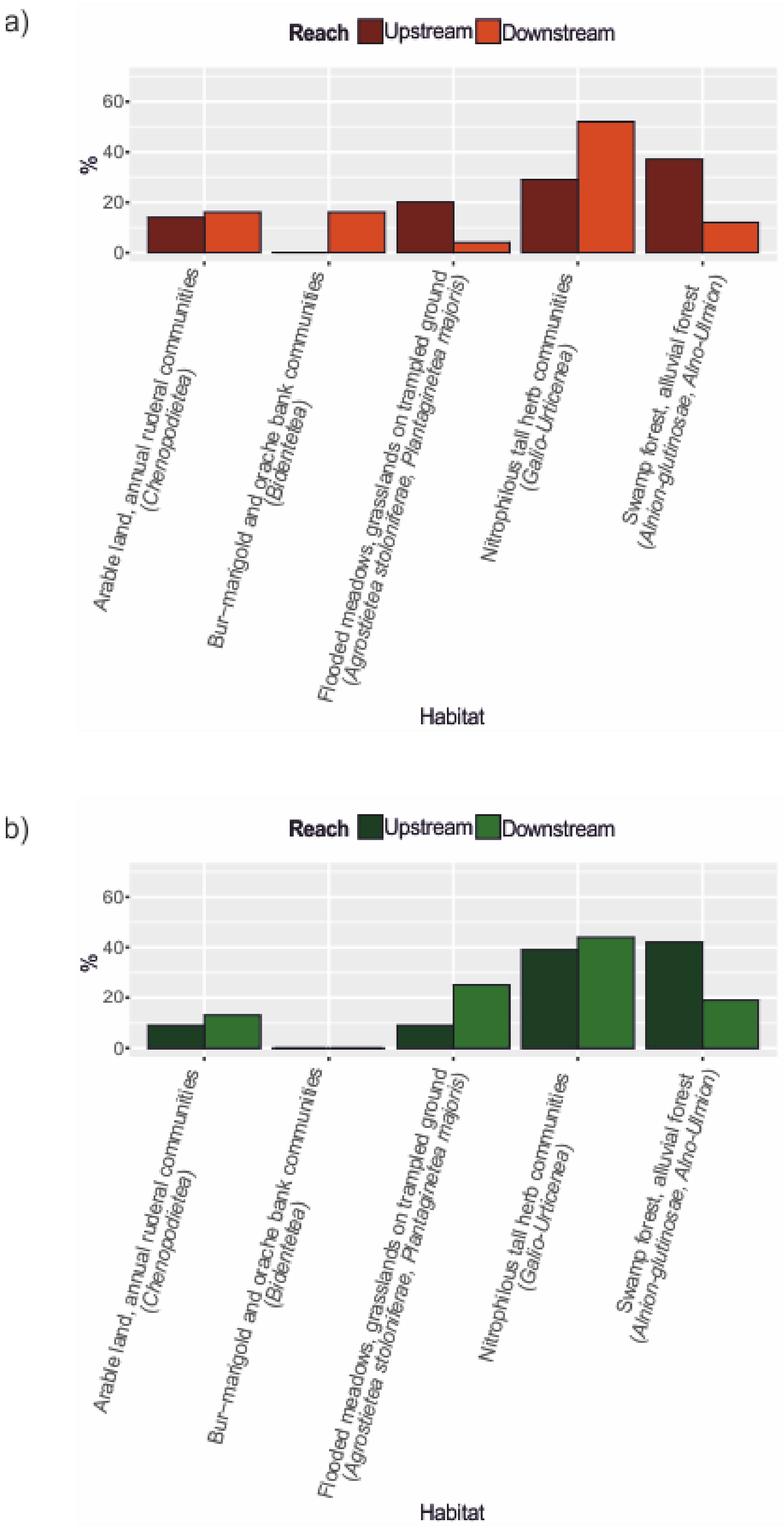

Fig. 3.5 - Habitat binding of significant and not significant indicator species for upstream and downstream reaches for relevant habitats, displayed by bars covering percentage values (Figure a): Lahn, Figure b): Fulda). Detailed information on species identity is provided in Table A3.9. Due to partly multiple species responses in different habitats, species´ main occurrences only in relevant habitats are displayed (Data extracted from FloraWeb (KORNECK ET AL. 1998); multiple answers possible).

3.3.2 Species´ ecological and functional traits

Compared to frequent occurrences of c-strategists along both rivers, r- and cr-strategists occurred rarely (Table 3.4). However, species´ life strategy was different upstream and downstream. At the Lahn, c-strategists were more common along the upstream reaches than downstream, where cr- and r-strategists became more important. Along the Fulda, r-strategists were also more common downstream, whereas cs-strategists dominated upstream. Patterns for c- and cr-strategists depending on the reach location were not detectable.

Irrespective of the weir reach, perennial species were very common along both rivers. Nonetheless, proportion of perennials was higher upstream, whereas annual species gained more in importance downstream.

Table 3.4 - Life strategies and longevity of reach-associated species, indicated by percentage values. Reach-associated species were determined by indicator species analysis and listed in Table A3.3 (Lahn) and Table A3.5 (Fulda) in the supporting information, that provides also detailed information on species affiliation to specification of the analysed traits (Table A3.7: Life strategy; Table A3.8: Longevity). Species´ life strategies are based on the csr-concept after GRIME (1979) (c=competitors, r=ruderal, s=stress tolerators and combinations thereof).

		Lahn		**Fulda**	
Trait	**Specification**	**Upstream (71 species)**	**Downstream (37 species)**	**Upstream (51 species)**	**Downstream (21 species)**
Life strategy	c (%)	52.1	36.1	52.0	52.4
	s (%)	0.0	0.0	0.0	0.0
	r (%)	2.8	8.3	0.0	4.8
	cs (%)	15.5	16.7	22.0	9.5
	cr (%)	9.9	25.0	10.0	9.5
	rs (%)	0.0	0.0	0.0	0.0
	csr (%)	19.7	13.9	16.0	23.8
Longevity	Annuals (%)	9.9	29.7	5.9	9.5
	Biennals (%)	4.2	2.7	3.9	9.5
	Perennials (%)	85.9	67.6	90.2	81.0

3.4 Discussion

3.4.1 Differences in upstream and downstream species composition

NMS results for the Fulda illustrate clear differences in upstream and downstream species composition and a higher association of downstream relevés to water level fluctuations. Although this pattern was less distinct for the Lahn data, the statistical comparison of the mean yearly water level fluctuation revealed that also the Lahn downstream reaches are governed by significantly higher water level fluctuations than upstream. Thus, downstream reaches are associated with higher lateral connectivity, a higher degree of disturbances by alternating water levels and a larger aquatic-terrestrial transition zone despite significantly steeper banks downstream than upstream along both rivers. The intensity and frequency of floods is one of the major determinants for high habitat heterogeneity in and along unregulated rivers, thus being the main driving factor for the high species turnover and for the vegetation structure in riparian zones (NAIMAN ET AL., 1993). The fact that species composition is more strongly determined by water level fluctuations than by bank inclination underlines the still high importance of this factor for the structure of riparian zones along regulated rivers.

Results of the indicator species analysis displayed relations to constant water levels for the upstream vegetation. Along the Lahn, this is indicated by *Filipendula ulmaria*, *Alnus glutinosa* and *Humulus lupulus*, in Germany originally occurring in swamp forests that are characterized by constant water levels (OBERDORFER, 1992b). Constant water levels are further displayed by *Vicia sepium*, *Stellaria graminea*, *Heracleum sphondylium* and *Sambucus nigra*. By contrast to *Filipendula ulmaria*, *Alnus glutinosa* and *Humulus lupulus*, these species exhibit only mesic moisture levels. This finding implies that the transition zone from water to land is narrow, thus enabling species with a wide amplitude towards moisture demands to occur in short distances to each other. Mesic moisture levels point to terrestrialization tendencies because of reduced disturbance by water level fluctuations (CATFORD ET AL., 2014). This enables competitive species like *Poa pratensis* and *Achillea millefolium* to establish also populations close to the river, although they occur naturally in some distance to rivers (FEDERAL AGENCY FOR NATURE CONSERVATION, 2011). In this way, species being adapted to water level fluctuations but exhibiting weak competitiveness are outcompeted. As regulation measures like deepening of the riverbed and the installation of weirs lead to disturbances of the natural flooding regime (CATFORD ET AL., 2014; MAHESHWARI ET AL., 1995), terrestrialization is a widespread phenomenon along regulated rivers (HARVOLK ET AL., 2015) and also present downstream. Due to the higher bank steepness along the Lahn upstream reaches (18%), we assume that this process is more strongly pronounced at the Lahn upstream reaches than along the Fulda upstream reaches (13%), which might also explain the absence of species with mesic moisture demands in the results of the Fulda indicator species analysis.

Constant water levels along the Fulda upstream reaches were displayed by species from reeds of still waters (*Phragmitetum australis*) like *Phragmites australis* and *Lycopus europaeus* (OBERDORFER, 1992a), showing analogies to lentic ecosystems. The resulting expansion of indicative species like *Phragmites australis* along impounded reaches was also proved by MAHESHWARI ET AL. (1995) and CESCHIN ET AL. (2015).

By contrast to upstream reaches, downstream species composition indicated more dynamic conditions. This finding is supported by the significant indicator species *Phalaris arundinacea* with a natural occurrence in reeds of flowing waters (*Phalaridetum arundinaceae*) (OBERDORFER, 1992a).

The observed differences in riparian vegetation due to differences in hydrological dynamics caused by impoundments were also observed by WISSKIRCHEN & HORCHLER (2017) along the river Mosel. Similar to our study they also identified specific indicator species that display the prevalent site conditions in direct proximity to impoundments well. Their results and our results imply that riparian plant communities are subject to distinct changes in species composition. This is mainly reflected by species of swamp forests, lentic ecosystems but also by species with mesic moisture levels, which occur upstream near to the river and which originally occur in larger distance to the river channel.

Our results also show that riverbank vegetation did not change with increasing distance to the weir, neither upstream nor downstream, which implies the extensive impact of weirs on riparian vegetation. This finding is in accordance with the fact that the impounded stretch is longer than 1000 m and that the influence of the weir does not cease gradually, at least within the stretch we studied. Transition zones are farther away from the weir and might even be absent in rivers with many weirs close to each other.

3.4.2 Upstream and downstream species show differences in functional responses to hydrological conditions

Differences in hydrological site conditions were also reflected in species´ life strategies, which are generally driven by disturbance events and resource availability (GRIME, 1979). Accordingly, habitats not likely to experience disturbances but with optimum resource availability are dominated by c-strategists, resulting in high competition between individuals. This is more the case for the upstream reaches, as the observed share of competitive species was at least at the Lahn upstream reaches higher. Although this finding could not be proved for the Fulda upstream reaches, a higher proportion of perennial species along upstream reaches of both rivers indicates that these habitats are able to develop later stages of succession (STROMBERG ET AL., 2007). Thus, functional traits of species occurring in direct proximity upstream of weirs reflect well lower disturbance levels by water level fluctuations.

By contrast, habitats generally being exposed to high disturbance levels are populated by a higher proportion of weak-competitive species following r-strategy that exhibit fast growth rates, high seed production and reduced life span (GRIME, 1979). Our results suggest that downstream vegetation is subject to a higher disturbance level as the observed number of r-strategists along both rivers and the observed numbers of cr-strategists at least at the Lahn was higher than upstream. Interestingly, this effect was not very pronounced along the Fulda. We explain this fact with a relatively higher bank steepness along the Fulda downstream reaches compared to the Lahn downstream reaches, which masks the effect of water level fluctuations for the most part. Our results regarding species´ functional responses in direct proximity to impoundments are well in line with WISSKIRCHEN & HORCHLER (2017), who also observed functional responses of species downstream of impoundments along the river Mosel.

Species´ response to river regulation by weirs might also vary depending on the local site conditions along the weirs. Along the Fulda, this is implied by a distinctly higher proportion of cs-strategists along the upstream reaches compared to the downstream reaches, whereas differences for the Lahn were not detectable. Cs-strategists are able to cope better with stress, which results in low growth rates, larger life spans and low seed production (GRIME, 1979). To check for stress caused by sustained waterlogging, we analyzed species´ Ellenberg indicator values for moisture (ELLENBERG ET AL., 1991) for both groups of upstream cs-strategists. These revealed relatively higher moisture levels for cs-strategists upstream along the Fulda than for upstream cs-strategists along the Lahn, which appears to confirm sustained waterlogging. As banks along the Fulda upstream reaches were associated to more species from reeds of still waters and swamp forests due to less steeper banks, the stress levels along the Fulda upstream reaches are assumed to be higher than along the Lahn upstream reaches.

Transition zones from aquatic to terrestrial areas along unregulated rivers naturally consist of a high number of r- and cr-strategists, whereas c-strategists occur in just small numbers (OBERDORFER, 1993). The generally high proportion of c-strategists along both rivers and vice versa the low occurrences of r- and cr-strategists point to considerable shifts in competitive structures being existent in riparian plant communities along regulated rivers. This is also supported by our results of species´ longevity, as a high proportion of the recorded species along both rivers exhibited long life spans. These results clearly indicate that riparian plant communities along both rivers are generally affected by a high degree of regulation.

3.4.3 Remnant habitats for species related to hydrodynamics

The significant indicator species *Poa trivialis* and *Rumex obtusifolius* along the Fulda downstream reaches suggest that species composition downstream is governed to a higher degree by recurring flooding events than upstream. These species originate from plant communities that experience disturbances by periodical flooding (*Agrostietea stoloniferae*) (OBERDORFER, 1993) and point to the fact that seasonal water level fluctuations are still existent along rivers that are regulated by weirs.

Apart from species from reeds of flowing waters and flooded meadows, the *Bidentetea* riparian plant communities belong also to habitats being subject to hydrodynamics (OBERDORFER, 1993). These habitat types are currently in decline and mainly occur below the mean and the lowest water level during low water phases in summer (FEDERAL AGENCY FOR NATURE CONSERVATION, 2011; OBERDORFER, 1993). Due to a pluvial flow regime along both rivers, low water levels and thus occurrences of species from the *Bidentetea* alliance are expected to be present during summers. This applies in particular to the downstream reaches, where the yearly water level fluctuations are proved to be significantly higher than upstream. Although the mean water discharges of the years 2016 and 2017 were lower than the long-term mean water discharges from 1986-2015, *Bidentetea* species were rare and limited to *Erysimum cheiranthoides*, *Persicaria lapathifolia* and *Persicaria dubia* in our dataset. As most of the fieldwork in 2016 was conducted during June, it is very likely that we could not record species being related to the *Bidentetea* alliance. The mean water discharges were more than doubled as a consequence of heavy rainfalls in June 2016, compared to the long-term values from 1986-2015. Actually, our *Bidentetea* species findings originate from downstream reaches of the weirs in Fürfurt and Niederbiel, which exhibit only exceptionally a low bank steepness (6%) and which were sampled during our fieldwork in June and July 2017. This year was characterized by low water discharges in the first half of the year (FEDERAL WATERWAYS AND SHIPPING ADMINISTRATION, 2019), which is why occurrences of *Bidentetea* species are not unreasonable. Occurrences of *Bidentetea* species downstream of weirs suggest that water level fluctuations in direct proximity downstream of weirs are suitable to sustain remnant habitats for species of declining riparian plant communities along regulated rivers. Appararently, the positive effect of water level fluctuation for typical riparian species is limited as a consequence of too steep banks along the downstream reaches, which applies to both rivers. This effect is assumed to be even more pronounced along the Fulda downstream reaches, which are characterized by relatively steeper banks than the Lahn ones. This is supported by our analysis regarding species habitat binding, where species from the *Bidentetea* alliance were absent, although weather conditions during our field work in June 2017 were suitable for occurrences of *Bidentetea* species also along the Fulda. Our results on weaker functional responses of species along the Fulda downstream reaches support this statement.

3.4 Conclusions for the restoration management

Our study illustrates that reduced water level fluctuations as a consequence of river regulation by weirs led to distinct shifts in species composition of riparian plant communities, which also applies to species´ functional traits. As a result, typical riparian plant communities (*Bidentetea* alliance) are in decline (FEDERAL AGENCY FOR NATURE CONSERVATION, 2011). This stresses the high importance of water level fluctuations for the promotion and conservation of typical riparian plant species along regulated rivers (BAART ET AL., 2013). Thus, the degree of bank steepness downstream of weirs should attract more attention in the future planning of river impoundments. For the success of nature conservation efforts along strongly regulated rivers, we therefore highly recommend the restoration of water level fluctuations by decreasing bank steepness as this can promote the effect of water level fluctuations for vegetation. Our study shows that even water level fluctuations in direct weir proximity are suited to enrich riparian plant communities by typical riverine species along downstream reaches. It is largely known that riparian ecosystems are negatively affected by impoundments, which is why restoration measures included also the removement of impoundments along rivers in recent times (BELLMORE ET AL., 2017). Nevertheless, as the removal of impoundments probably cannot be realized entirely, our study illustrates important starting points for restoration measures along impounded rivers, which probably cannot be returned into an original state.

Decreasing bank steepness in direct proximity to weirs could also promote the spread of species to restoration measures located further downstream. This will especially apply to restoration measures, which are not located within two weirs. Potential effects for restoration measures located within two weirs will become weaker with decreasing distance to the next weir, as water level fluctuations will decline gradually. During the planning of restoration measures along impounded rivers, we therefore recommend to take the distance to the next weir into account. These measures offer options to enhance the ecological status of regulated rivers, thus getting closer to the goals of the Water Framework Directive, which aims to achieve a good ecological potential along regulated rivers.

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Appendix Chapter 3

Table A3.1 - Names and years of construction of the studied weirs along the Lahn and the Fulda.

River	Weir	Year of construction	Sampling time
Lahn	Dorlar	1848	June 2016
	Naunheim	1848	July/August 2017
	Biel	1848	July 2017
	Löhnberg	1846	August 2017
	Fürfurt	1859	June 2017
	Scheidt	1927	June 2016
Fulda	Neumorschen	1752	June 2016
	Melsungen	1752	June 2017
	Wilhelmshausen	1988	June 2016

Table A3.2 - Correlations of environmental variables with NMS-ordination axes for both rivers.

Waterway	Environmental variable	Axis 1 R^2	Axis 2 R^2	Axis 3 R^2
Lahn	Altitude	0.019	0.005	0.098
	Inclin	0.069	0.013	0.006
	Cov_tree	0.060	0.174	0.060
	Cov_shrub	0.002	0.075	0.026
	Cov_herb	0.018	0.020	0.012
	Cov_grass	0.034	0.064	0.037
	Cov_litter	0.040	0.008	0.051
	Cov_soil	0.006	0.014	0.012
	Richness	0.001	0.004	0.669
	Shannon	0.000	0.010	0.686
	Evenness	0.004	0.065	0.300
	Water level fluctuation	0.225	0.001	0.001
	EIV Light	0.130	0.027	0.260
	EIV Moisture	0.006	0.091	0.235
	EIV Nutrient	0.079	0.004	0.476
	P_2O_5	0.024	0.000	0.219
	K_2O	0.016	0.018	0.054
	Ctot	0.003	0.032	0.193
	Ntot	0.001	0.024	0.248
Fulda	Altitude	0.016	0.021	0.255
	Inclin	0.064	0.172	0.020
	Cov_tree	0.271	0.219	0.260
	Cov_shrub	0.000	0.044	0.035
	Cov_herb	0.119	0.002	0.038
	Cov_grass	0.101	0.094	0.000
	Cov_litter	0.000	0.171	0.245
	Cov_soil	0.017	0.183	0.158
	Richness	0.097	0.302	0.002
	Shannon	0.003	0.147	0.069
	Evenness	0.053	0.005	0.211
	Water level fluctuation	0.023	0.243	0.009
	EIV Light	0.070	0.249	0.059
	EIV Moisture	0.083	0.131	0.313
	EIV Nutrient	0.001	0.569	0.151
	P_2O_5	0.112	0.124	0.044

K_2O	0.012	0.239	0.001
Ctot	0.074	0.132	0.048
Ntot	0.090	0.095	0.054

Table A3.3 - Indicator species for upstream and downstream weir reaches for the Lahn. Significant indicator species are characterized by an indicator value (IV) >25 and a p-value <0.05 (Monte Carlo randomization test).

Reach	Species name	A (Specificity)	B (Sensitivity)	IV	p.value	Significance
Upstream	*Filipendula ulmaria*	0.72299	0.66667	0.694	0.001	***
	Aegopodium podagraria	0.78241	0.5	0.625	0.002	**
	Sambucus nigra	1	0.14583	0.382	0.015	*
	Stellaria graminea	1	0.125	0.354	0.026	*
	Heracleum sphondylium	0.92308	0.125	0.34	0.029	*
	Vicia sepium	1	0.125	0.354	0.03	*
	Rubus vulgaris	0.96296	0.16667	0.401	0.04	*
	Alnus glutinosa	0.79412	0.29167	0.481	0.041	*
	Circaea lutetiana	1	0.10417	0.323	0.056	.
	Equisetum arvense	0.80769	0.16667	0.367	0.057	.
	Lycopus europaeus	0.76923	0.1875	0.38	0.074	.
	Brachypodium sylvaticum	0.75	0.20833	0.395	0.081	.
	Acer pseudoplatanus	0.91837	0.125	0.339	0.09	.
	Calystegia sylvatica	1	0.08333	0.289	0.117	
	Taraxacum sect. Ruderalia	0.85714	0.10417	0.299	0.123	
	Festuca rubra	0.6381	0.14583	0.305	0.211	
	Clematis vitalba	1	0.0625	0.25	0.227	
	Epilobium hirsutum	0.76	0.125	0.308	0.229	
	Lolium perenne	0.88235	0.0625	0.235	0.229	
	Achillea millefolium	1	0.0625	0.25	0.233	
	Crataegus monogyna	1	0.0625	0.25	0.235	
	Holcus lanatus	0.875	0.0625	0.234	0.237	
	Prunus avium	1	0.0625	0.25	0.237	
	Poa pratensis	1	0.0625	0.25	0.238	
	Valeriana procurrens	1	0.0625	0.25	0.239	
	Fraxinus excelsior	0.75676	0.08333	0.251	0.312	
	Festuca arundinacea	0.65385	0.08333	0.233	0.358	
	Origanum vulgare	1	0.04167	0.204	0.475	
	Potentilla reptans	1	0.04167	0.204	0.475	
	Quercus robur	1	0.04167	0.204	0.483	
	Valeriana versifolia	1	0.04167	0.204	0.485	
	Dryopteris filix-mas	1	0.04167	0.204	0.487	
	Phleum pratense	1	0.04167	0.204	0.492	
	Bromus hordeaceus	1	0.04167	0.204	0.502	
	Fagus sylvatica	1	0.04167	0.204	0.502	
	Plantago lanceolata	1	0.04167	0.204	0.508	
	Stachys sylvatica	0.88462	0.08333	0.272	0.511	
	Galeopsis tetrahit	1	0.04167	0.204	0.523	
	Acer campestre	1	0.02083	0.144	1	
	Agrostis stolonifera	1	0.02083	0.144	1	
	Barbarea stricta	1	0.02083	0.144	1	
	Cardamine bulbifera	1	0.02083	0.144	1	
	Cardamine impatiens	1	0.02083	0.144	1	
	Carex acuta	1	0.02083	0.144	1	
	Chelidonium majus	1	0.02083	0.144	1	

	Cornus sanguinea	1	0.02083	0.144	1	
	Festuca gigantea	1	0.02083	0.144	1	
	Geranium molle	1	0.02083	0.144	1	
	Geranium pratense	1	0.02083	0.144	1	
	Hedera helix	1	0.02083	0.144	1	
	Melilotus indicus	1	0.02083	0.144	1	
	Myosotis sylvatica	1	0.02083	0.144	1	
	Papaver rhoeas	1	0.02083	0.144	1	
	Picris hieracioides	1	0.02083	0.144	1	
	Plantago major	1	0.02083	0.144	1	
	Potentilla anserina	1	0.02083	0.144	1	
	Prunus spinosa	1	0.02083	0.144	1	
	Ranunculus acris	1	0.02083	0.144	1	
	Ribes rubrum	1	0.02083	0.144	1	
	Rosa canina	1	0.02083	0.144	1	
	Rumex acetosa	1	0.02083	0.144	1	
	Salix aurita	1	0.02083	0.144	1	
	Sanguisorba officinalis	1	0.02083	0.144	1	
	Sorbus aucuparia	1	0.02083	0.144	1	
	Stellaria media	1	0.02083	0.144	1	
	Stellaria nemorum	1	0.02083	0.144	1	
	Trifolium medium	1	0.02083	0.144	1	
	Trifolium pratense	1	0.02083	0.144	1	
	Trifolium repens	1	0.02083	0.144	1	
	Verbascum nigrum	1	0.02083	0.144	1	
	Veronica serpyllifolia	1	0.02083	0.144	1	
Downstream	*Achillea ptarmica*	0.85294	0.20833	0.422	0.016	*
	Scrophularia nodosa	1	0.125	0.354	0.02	*
	Helianthus tuberosus	1	0.10417	0.323	0.066	.
	Solanum dulcamara	0.90909	0.10417	0.308	0.092	.
	Vicia cracca	0.7931	0.14583	0.34	0.145	
	Brassica nigra	0.875	0.10417	0.302	0.148	
	Cuscuta europaea	0.78788	0.125	0.314	0.216	
	Epilobium palustre	0.96721	0.0625	0.246	0.223	
	Mentha aquatica	1	0.0625	0.25	0.262	
	Juncus effusus	0.82353	0.0625	0.227	0.481	
	Quercus petraea	1	0.04167	0.204	0.486	
	Epilobium obscurum	1	0.04167	0.204	0.493	
	Oxalis stricta	1	0.04167	0.204	0.495	
	Bidens frondosa	1	0.04167	0.204	0.497	
	Persicaria lapathifolia	1	0.04167	0.204	0.497	
	Persicaria dubia	1	0.04167	0.204	0.498	
	Anthriscus sylvestris	1	0.04167	0.204	0.506	
	Carpinus betulus	0.97297	0.04167	0.179	0.507	
	Linaria vulgaris	1	0.04167	0.144	0.515	
	Epilobium ciliatum	0.76923	0.04167	0.144	0.748	
	Ballota nigra	1	0.02083	0.144	1	
	Carex acuta	1	0.02083	0.144	1	
	Chenopodium album	1	0.02083	0.144	1	
	Conyza canadensis	1	0.02083	0.144	1	
	Cruciata laevipes	1	0.02083	0.144	1	
	Epilobium parviflorum	1	0.02083	0.144	1	
	Erysimum cheiranthoides	1	0.02083	0.144	1	
	Eupatorium cannabinum	1	0.02083	0.144	1	

Hypericum hirsutum	1	0.02083	0.144	1
Matricaria recutita	1	0.02083	0.144	1
Melilotus officinalis	1	0.02083	0.144	1
Prunus padus	1	0.02083	0.144	1
Ranunculus ficaria	1	0.02083	0.144	1
Salix purpurea	1	0.02083	0.144	1
Stellaria palustris	1	0.02083	0.144	1
Thlaspi arvense	1	0.02083	0.144	1
Vicia villosa	1	0.02083	0.144	1

Table A3.4 - Species without specific weir reach association at the Lahn (determined by indicator species analysis). IV= indicator value, index=3 refers to the combination of upstream and downstream reaches.

Species name	Upstream	Downstream	index	IV	p.value
Alliaria petiolata	1	1	3	0.66143783	NA
Acer platanoides	1	1	3	0.14433757	NA
Agrostis capillaris	1	1	3	0.14433757	NA
Alopecurus pratensis	1	1	3	0.32274861	NA
Arctium lappa	1	1	3	0.27003086	NA
Arctium minus	1	1	3	0.20412415	NA
Arrhenatherum elatius	1	1	3	0.5	NA
Artemisia vulgaris	1	1	3	0.45643546	NA
Barbarea vulgaris	1	1	3	0.14433757	NA
Bromus inermis	1	1	3	0.45643546	NA
Bromus sterilis	1	1	3	0.20412415	NA
Calystegia sepium	1	1	3	0.85391256	NA
Carduus cripsus	1	1	3	0.60380736	NA
Chaerophyllum bulbosum	1	1	3	0.70710678	NA
Chaerophyllum temulum	1	1	3	0.22821773	NA
Cirsium arvense	1	1	3	0.27003086	NA
Cirsium oleraceum	1	1	3	0.14433757	NA
Corylus avellana	1	1	3	0.27003086	NA
Dactylis glomerata	1	1	3	0.5	NA
Elymus caninus	1	1	3	0.28867513	NA
Elymus repens	1	1	3	0.61237244	NA
Euonymus europaeus	1	1	3	0.14433757	NA
Fallopia convolvulus	1	1	3	0.14433757	NA
Galeopsis pubescens	1	1	3	0.14433757	NA
Galium aparine	1	1	3	0.8291562	NA
Galium mollugo	1	1	3	0.54006172	NA
Geranium robertianum	1	1	3	0.30618622	NA
Geum urbanum	1	1	3	0.38188131	NA
Glechoma hederacea	1	1	3	0.64549722	NA
Glyceria maxima	1	1	3	0.14433757	NA
Heracleum mantegazzianum	1	1	3	0.14433757	NA
Humulus lupulus	1	1	3	0.46770717	NA
Hypericum perforatum	1	1	3	0.28867513	NA
Impatiens glandulifera	1	1	3	0.93541435	NA
Iris pseudacorus	1	1	3	0.27003086	NA
Lamium album	1	1	3	0.4330127	NA
Lamium maculatum	1	1	3	0.75691259	NA
Lamium purpureum	1	1	3	0.14433757	NA
Lapsana communis	1	1	3	0.20412415	NA
Lysimachia vulgaris	1	1	3	0.59511904	

Lythrum salicaria	1	1	3	0.62915287	NA
Persicaria amphibia	1	1	3	0.1767767	NA
Phalaris arundinacea	1	1	3	0.72886899	NA
Phragmites australis	1	1	3	0.59511904	NA
Poa palustris	1	1	3	0.56825757	NA
Poa trivialis	1	1	3	0.66143783	NA
Ranunculus repens	1	1	3	0.36799004	NA
Rorippa amphibia	1	1	3	0.25	NA
Rubus caesius	1	1	3	0.63737744	NA
Rumex crispus	1	1	3	0.14433757	NA
Rumex sanguineus	1	1	3	0.27003086	NA
Salix alba	1	1	3	0.3385016	NA
Salix fragilis	1	1	3	0.62915287	NA
Salix triandra	1	1	3	0.22821773	NA
Salix viminalis	1	1	3	0.25	NA
Saponaria officinalis	1	1	3	0.14433757	NA
Scrophularia auriculata	1	1	3	0.28867513	NA
Scrophularia umbrosa	1	1	3	0.22821773	NA
Scutellaria galericulata	1	1	3	0.30618622	NA
Silene dioica	1	1	3	0.5204165	NA
Stachys palustris	1	1	3	0.44487826	NA
Stellaria aquatica	1	1	3	0.30618622	NA
Symphytum officinale	1	1	3	0.32274861	NA
Tanacetum vulgare	1	1	3	0.32274861	NA
Urtica dioica	1	1	3	0.98952851	NA
Valeriana officinalis	1	1	3	0.3385016	NA
Vicia hirta	1	1	3	0.14433757	NA
					NA

Table A3.5 - Indicator species for upstream and downstream weir reaches for the Fulda. Significant indicator species are characterized by an indicator value (IV) >25 and a p-value <0.05 (Monte Carlo randomization test).

Reach	Species name	A (Specificity)	B (Sensitivity)	IV	p.value	Significance
Upstream	*Filipendula ulmaria*	0.87402	0.66667	0.763	0.001	***
	Humulus lupulus	0.85938	0.375	0.568	0.012	*
	Phragmites australis	0.79773	0.5	0.632	0.02	*
	Lycopus europaeus	0.76667	0.45833	0.593	0.022	*
	Alopecurus pratensis	0.81818	0.375	0.554	0.037	*
	Lamium album	0.80645	0.33333	0.518	0.059	.
	Dactylis glomerata	0.83636	0.33333	0.528	0.06	.
	Fraxinus excelsior	0.86919	0.29167	0.504	0.071	.
	Stellaria graminea	1	0.16667	0.408	0.113	
	Alnus glutinosa	0.76021	0.25	0.436	0.158	
	Epilobium hirsutum	1	0.125	0.354	0.22	
	Lapsana communis	0.83333	0.16667	0.373	0.236	
	Holcus lanatus	0.88235	0.125	0.332	0.24	
	Galium mollugo	0.85	0.16667	0.376	0.275	
	Scrophularia umbrosa	0.86667	0.125	0.329	0.334	
	Solanum dulcamara	0.72727	0.16667	0.348	0.344	
	Crataegus monogyna	1	0.08333	0.289	0.456	
	Hedera helix	1	0.08333	0.289	0.481	
	Salix triandra	1	0.08333	0.289	0.482	
	Hypericum tetrapterum	1	0.08333	0.289	0.487	

	Sambucus nigra	1	0.08333	0.289	0.489	
	Vicia sepium	1	0.08333	0.289	0.49	
	Cuscuta europaea	1	0.08333	0.289	0.501	
	Scrophularia nodosa	0.75	0.125	0.253	0.618	
	Carduus nutans	0.76923	0.04167	0.204	0.736	
	Acer campestre	1	0.04167	0.204	1	
	Achillea millefolium	1	0.04167	0.204	1	
	Bromus arvensis	1	0.04167	0.204	1	
	Calamintha menthifolia	1	0.04167	0.204	1	
	Chelidonium majus	1	0.04167	0.204	1	
	Cornus sanguinea	1	0.04167	0.204	1	
	Corylus avellana	1	0.04167	0.204	1	
	Cruciata laevipes	1	0.04167	0.204	1	
	Dryopteris filix-mas	1	0.04167	0.204	1	
	Epilobium roseum	1	0.04167	0.204	1	
	Equisetum arvense	1	0.04167	0.204	1	
	Fallopia sachalinensis	1	0.04167	0.204	1	
	Festuca rubra	1	0.04167	0.204	1	
	Lonicera xylosteum	1	0.04167	0.204	1	
	Lysimachia nummularia	1	0.04167	0.204	1	
	Myosotis laxa	0.75	0.04167	0.25	1	
	Phleum pratense	1	0.04167	0.204	1	
	Plantago lanceolata	1	0.04167	0.204	1	
	Plantago major	1	0.04167	0.204	1	
	Ranunculus acris	1	0.04167	0.204	1	
	Rhamnus cathartica	1	0.04167	0.204	1	
	Ribes rubrum	1	0.04167	0.204	1	
	Sanguisorba officinalis	1	0.04167	0.204	1	
	Scrophularia auriculata	1	0.04167	0.204	1	
	Veronica beccabunga	1	0.04167	0.204	1	
	Viola hirta	1	0.04167	0.204	1	
Downstream	*Phalaris arundinacea*	0.8317	0.95833	0.893	0.001	***
	Poa trivialis	0.8	0.5	0.632	0.011	*
	Rumex obtusifolius	1	0.25	0.5	0.015	*
	Calystegia sylvatica	0.8	0.16667	0.365	0.206	
	Solidago canadensis	1	0.125	0.354	0.217	
	Epilobium palustre	0.97802	0.125	0.35	0.231	
	Sonchus asper	1	0.125	0.354	0.234	
	Heracleum mantegazzianum	1	0.08333	0.289	0.459	
	Ranunculus ficaria	1	0.08333	0.289	0.482	
	Symphytum officinale	1	0.08333	0.289	0.482	
	Agrostis capillaris	1	0.04167	0.204	1	
	Angelica archangelica	1	0.04167	0.204	1	
	Cirsium oleraceum	1	0.04167	0.204	1	
	Fallopia convolvulus	1	0.04167	0.204	1	
	Glyceria fluitans	1	0.04167	0.204	1	
	Juglans regia	1	0.04167	0.204	1	
	Nepeta cataria	1	0.04167	0.204	1	
	Oxalis stricta	1	0.04167	0.204	1	
	Rumex acetosa	1	0.04167	0.204	1	
	Tanacetum vulgare	1	0.04167	0.204	1	
	Trifolium repens	1	0.04167	0.204	1	

Table A3.6 - Species without specific weir reach association at the Fulda (determined by indicator species analysis). IV= indicator value, index=3 refers to the combination of upstream and downstream reaches.

Species name	Upstream	Downstream	index	IV	p.value
Alliaria petiolata	1	1	3	0.90138782	NA
Acer platanoides	1	1	3	0.35355339	NA
Acer pseudoplatanus	1	1	3	0.20412415	NA
Achillea ptarmica	1	1	3	0.20412415	NA
Aegopodium podagraria	1	1	3	0.76376262	NA
Arctium lappa	1	1	3	0.35355339	NA
Arctium minus	1	1	3	0.28867513	NA
Arrhenatherum elatius	1	1	3	0.59511904	NA
Artemisia verlotiorum	1	1	3	0.5204165	NA
Artemisia vulgaris	1	1	3	0.28867513	NA
Bromus inermis	1	1	3	0.66143783	NA
Calystegia sepium	1	1	3	0.88975652	NA
Carduus crispus	1	1	3	0.57735027	NA
Chaerophyllum bulbosum	1	1	3	0.88975652	NA
Chaerophyllum temulum	1	1	3	0.32274861	NA
Circaea lutetiana	1	1	3	0.61237244	NA
Cirsium arvense	1	1	3	0.38188131	NA
Elymus caninus	1	1	3	0.45643546	NA
Elymus repens	1	1	3	0.66143783	NA
Festuca arundincea	1	1	3	0.35355339	NA
Festuca gigantea	1	1	3	0.40824829	NA
Galeopsis pubenscens	1	1	3	0.55901699	NA
Galium aparine	1	1	3	0.90138782	NA
Geranium robertianum	1	1	3	0.20412415	NA
Geum urbanum	1	1	3	0.55901699	NA
Glechoma hederacea	1	1	3	0.66143783	NA
Glyceria maxima	1	1	3	0.20412415	NA
Heracleum sphondylium	1	1	3	0.28867513	NA
Impatiens glandulifera	1	1	3	0.93541435	NA
Iris pseudacorus	1	1	3	0.38188131	NA
Lamium maculatum	1	1	3	0.77728159	NA
Lysimachia vulgaris	1	1	3	0.54006172	NA
Lythrum salicaria	1	1	3	0.54006172	NA
Mentha aquatica	1	1	3	0.25	NA
Persicaria amphibia	1	1	3	0.25	NA
Plantago media	1	1	3	0.25	NA
Poa palustris	1	1	3	0.8660254	NA
Ranuculus repens	1	1	3	0.28867513	NA
Rorippa amphibia	1	1	3	0.35355339	NA
Rorippa x anceps	1	1	3	0.20412415	NA
Rubus caesius	1	1	3	0.66143783	NA
Rumex sanguineus	1	1	3	0.47871355	NA
Salix fragilis	1	1	3	0.73598007	NA
Salix purpurea	1	1	3	0.20412415	NA
Scutellaria galericulata	1	1	3	0.32274861	NA
Silene dioica	1	1	3	0.62915287	NA
Stachys palustris	1	1	3	0.32274861	NA
Stachys sylvatica	1	1	3	0.4330127	NA
Stellaria aquatica	1	1	3	0.5204165	

Taraxacum sect. Ruderalia	1	1	3	0.20412415	NA
Ulmus minor	1	1	3	0.20412415	NA
Urtica dioica	1	1	3	0.98952851	NA
Vicia cracca	1	1	3	0.32274861	NA
					NA

Table A3.7 - Reach-associated species (determined by indicator species analysis) classified by their life strategy after GRIME (1979) (c=competitors, r=ruderal, s=stress tolerators and combinations thereof) that were considered for species´ trait analysis for the Lahn and Fulda (Data extracted from BiolFlor (KÜHN ET AL., 2004)). Species, for which information on life strategy was not available are listed as "Other" (no statistical consideration).

		Lahn		Fulda	
Reach	Classification	Species	Percentage	Species	Percentage
Upstream	c-strategists	*Filipendula ulmaria*	52.1	*Vicia sepium*	52.0
		Aegopodium podagraria		*Solanum dulcamara*	
		Sambucus nigra		*Sambucus nigra*	
		Heracleum sphondylium		*Salix triandra*	
		Vicia sepium		*Ribes rubrum*	
		Rubus vulgaris		*Rhamnus cathartica*	
		Alnus glutinosa		*Ranunculus acris*	
		Acer pseudoplatanus		*Phleum pratense*	
		Calystegia sylvatica		*Lonicera xylosteum*	
		Festuca rubra		*Humulus lupulus*	
		Clematis vitalba		*Holcus lanatus*	
		Epilobium hirsutum		*Galium mollugo*	
		Lolium perenne		*Fraxinus excelsior*	
		Achillea millefolium		*Filipendula ulmaria*	
		Crataegus monogyna		*Festuca rubra*	
		Holcus lanatus		*Fallopia sachalinensis*	
		Prunus avium		*Epilobium hirsutum*	
		Poa pratensis		*Dactylis glomerata*	
		Valeriana procurrens		*Crataegus monogyna*	
		Fraxinus excelsior		*Corylus avellana*	
		Festuca arundinacea		*Cornus sanguinea*	
		Quercus robur		*Calamintha menthifolia*	
		Phleum pratense		*Alopecurus pratensis*	
		Fagus sylvatica		*Alnus glutinosa*	
		Acer campestre		*Achillea millefolium*	
		Cornus sanguinea		*Acer campestre*	
		Geranium pratense			
		Prunus spinosa			
		Ranunculus acris			

	Ribes rubrum *Rosa canina* *Rumex acetosa* *Salix aurita* *Sorbus aucuparia* *Trifolium medium* *Trifolium pratense* *Verbascum nigrum*			
s-strategists	-	0.0	-	0.0
r-strategists	*Geranium molle* *Melilotus indicus*	2.8	-	0.0
cs-strategists	*Stellaria graminea* *Circaea lutetiana* *Lycopus europaeus* *Brachypodium sylvaticum* *Valeriana versifolia* *Dryopteris filix-mas* *Stachys sylvatica* *Carex acutiformis* *Festuca gigantea* *Hedera helix* *Sanguisorba officinalis*	15.5	*Veronica beccabunga* *Stellaria graminea* *Scrophularia umbrosa* *Scrophularia nodosa* *Scrophularia auriculata* *Sanguisorba officinalis* *Phragmites australis* *Lycopus europaeus* *Hedera helix* *Epilobium roseum* *Dryopteris filix-mas*	22.0
cr-strategists	*Equisetum arvense* *Bromus hordeaceus* *Galeopsis tetrahit* *Barbarea stricta* *Chelidonium majus* *Papaver rhoeas* *Stellaria media*	9.9	*Lapsana communis* *Equisetum arvense* *Chelidonium majus* *Carduus nutans* *Bromus arvensis*	10.0
rs-strategists	-	0	-	0
csr-strategists	*Taraxacum sect. Ruderalia* *Origanum vulgare* *Potentilla reptans* *Plantago lanceolata*	19.7	*Viola hirta* *Plantago major* *Plantago lanceolata* *Myosotis laxa*	16.0

		Agrostis stolonifera		*Lysimachia nummularia*	
		Cardamine bulbifera		*Lamium album*	
		Cardamine impatiens		*Hypericum tetrapterum*	
		Myosotis sylvatica		*Cruciata laevipes*	
		Picris hieracoides			
		Plantago major			
		Potentilla anserina			
		Stellaria nemorum			
		Trifolium repens			
		Veronica serpyllifolia			
	Other	-		*Cuscuta europaea*	
Downstream	c-strategists	*Helianthus tuberosus*	36.1	*Phalaris arundinacea*	52.4
		Solanum dulcamara		*Rumex obtusifolius*	
		Vicia cracca		*Calystegia sylvatica*	
		Juncus effusus		*Solidago canadensis*	
		Quercus petraea		*Heracleum mantegazzianum*	
		Anthriscus sylvestris		*Sympyhtum officinale*	
		Carpinus betulus		*Cirsium oleraceum*	
		Epilobium ciliatum		*Juglans regia*	
		Ballota nigra		*Nepeta cataria*	
		Eupatorium cannabinum		*Rumex acetosa*	
		Hypericum hirsutum		*Tanacetum vulgare*	
		Prunus padus			
		Salix purpurea			
	s-strategists	-	0.0	-	0.0
	r-strategists	*Oxalis stricta*	8.3	*Oxalis stricta*	4.8
		Matricaria recutita			
		Thlaspi arvense			
	cs-strategists	*Achillea ptarmica*	16.7	*Angelica archangelica*	9.5
		Scrophularia nodosa		*Glyceria fluitans*	
		Mentha aquatica			
		Epilobium obscurum			
		Carex acuta			
		Epilobium parviflorum			

	cr-strategists	*Brassica nigra* *Bidens frondosa* *Persicaria lapathifolia* *Persicaria dubia* *Chenopodium album* *Conyza canadensis* *Erysimum cheiranthoides* *Melilotus officinalis* *Vicia villosa*	25.0	*Sonchus asper* *Fallopia convolvulus*	9.5
	rs-strategists	-	0	-	0
	csr-strategists	*Epilobium palustre* *Linaria vulgaris* *Crucitata laevipes* *Ranunculus ficaria* *Stellaria palustris*	13.9	*Poa trivialis* *Epilobium palustre* *Ranunculus ficaria* *Agrostis capillaris* *Trifolium repens*	23.8
	Other	*Cuscuta europaea*		-	

Table A3.8 - Reach-associated species (determined by indicator species analysis) classified by their longevity (a=annuals, b=biennials, p=perennials) that were considered for species´ trait analysis for the Lahn and the Fulda (Data extracted from BiolFlor (KÜHN ET AL., 2004)).

		Lahn		Fulda	
Reach	Classification	Species	Percentage	Species	Percentage
Upstream	a	*Bromus hordeaceus* *Galeopsis tetrahit* *Cardamine impatiens* *Geranium molle* *Melilotus indicus* *Papaver rhoeas* *Stellaria media*	9.9	*Lapsana communis* *Cuscuta europea* *Bromus arvensis*	5.9
	b	*Barbarea stricta* *Picris hieracioides* *Verbascum nigrum*	4.2	*Carduus nutans* *Myosotis laxa*	3.9
	p	*Filipendula ulmaria* *Aegopodium podagraria*	85.9	*Filipendula ulmaria* *Humulus lupulus*	90.2

Sambucus nigra	*Phragmites australis*
Stellaria graminea	*Lycopus europaeus*
Heracleum sphondylium	*Alopecurus pratensis*
Vicia sepium	*Lamium album*
Rubus vulgaris	*Dactylis glomerata*
Alnus glutinosa	*Fraxinus excelsior*
Circaea lutetiana	*Stellaria graminea*
Equisetum arvense	*Alnus glutinosa*
Lycopus europaeus	*Epilobium hirsutum*
Brachypodium sylvaticum	*Holcus lanatus*
Acer pseudoplatanus	*Galium mollugo*
Calystegia silvatica	*Scrophularia umbrosa*
Taraxacum sect. Ruderalia	*Solanum dulcamara*
Festuca rubra	*Crataegus monogyna*
Clematis vitalba	*Hedera helix*
Epilobium hirsutum	*Salix triandra*
Lolium perenne	*Hypericum tetrapterum*
Achillea millefolium	*Sambus nigra*
Crataegus monogyna	*Vicia sepium*
Holcus lanatus	*Scrophularia nodosa*
Prunus avium	*Acer campestre*
Poa pratensis	*Achillea millefolium*
Valeriana procurrens	*Calamintha menthifolia*
Fraxinus excelsior	*Chelidonium majus*
Festuca arundinacea	*Cornus sanguinea*
Origanum vulgare	*Corylus avellana*
Potentilla reptans	*Cruciata laevipes*
Quercus robur	*Dryopteris filix-mas*
Valeriana versifolia	*Epilobium roseum*
Dryopteris filix-mas	*Equisetum arvense*
Phleum pratense	*Fallopia sachalinensis*
Fagus sylvatica	*Festuca rubra*
Plantago lanceolata	*Lonicera xylosteum*
Stachys sylvatica	*Lysimachia nummularia*

		Acer campestre *Agrostis stolonifera* *Cardamine bulbifera* *Carex acutiformis* *Chelidonium majus* *Cornus sanguinea* *Festuca gigantean* *Geranium pratense* *Hedera helix* *Myosotis sylvatica* *Plantago major* *Potentilla anserina* *Prunus spinosa* *Ranunculus acris* *Ribes rubrum* *Rosa canina* *Rumex acetosa* *Salix aurita* *Sanguisorba officinalis* *Sorbus aucuparia* *Stellaria nemorum* *Trifolium medium* *Trifolium pratense* *Trifolium repens* *Veronica serpyllifolia*		*Phleum pratense* *Plantago lanceolata* *Plantago major* *Ranunculus acris* *Rhamnus cathartica* *Ribes rubrum* *Sanguisorba officinalis* *Scrophualria auriculata* *Veronica beccabunga* *Viola hirta*	
Downstream	a	*Brassica nigra* *Cuscuta europaea* *Bidens frondosa* *Persicaria lapathifolia* *Persicaria dubia* *Chenopodium album* *Conyza canadensis* *Erysimum cheiranthoides* *Matricaria recutita*	29.7	*Sonchus asper* *Fallopia convolvulus*	9.5

	Thlaspi arvense *Vicia villosa*			
b	*Melilotus officinalis*	2.7	*Heracleum mantegazzianum* *Angelica archangelica*	9.5
p	*Achillea ptarmica* *Scrophuria nodosa* *Helianthus tuberosus* *Solanum dulcamara* *Vicia cracca* *Epilobium palustre* *Mentha aquatica* *Juncus effusus* *Quercus petraea* *Epilobium obscurum* *Oxalis stricta* *Anthriscus sylvestris* *Carpinus betulus* *Linaria vulgaris* *Epilobium ciliatum* *Ballota nigra* *Carex acuta* *Cruciata laevipes* *Epilobium parviflorum* *Eupatorium cannabinum* *Hypericum hirsutum* *Prunus padus* *Ranunculus ficaria* *Salix purpurea* *Stellaria palustris*	67.6	*Phalaris arundinacea* *Poa trivialis* *Rumex obtusifolius* *Calystegia silvatica* *Solidago canadensis* *Epilobium palustre* *Ranuculus ficara* *Symphytum officinale* *Agrostis capillaris* *Cirsium oleraceum* *Glyceria fluitans* *Juglans regia* *Nepeta cataria* *Oxalis stricta* *Rumex acetosa* *Tanacetum vulgare* *Trifolium repens*	81.0

Table A3.9 - Reach-associated species (determined by indicator species analysis) classified by their habitat origin that were considered for species´ trait analysis for the Lahn and Fulda (Data extracted from FloraWeb (KORNECK ET AL., 1998)).

		Lahn		Fulda	
Reach	Habitat	Species	Percentage	Species	Percentage
Upstream	Nitrophilous tall herb communities	*Aegopodium podagraria*	29.4	*Humulus lupulus*	39.4
	(*Galio-Urticenea*)	*Sambucus nigra*		*Lamium album*	
		Heracleum sphondylium		*Dactylis glomerata*	
		Vicia sepium		*Lapsana communis*	
		Poa pratensis		*Galium mollugo*	
		Stachys sylvatica		*Solanum dulcamara*	
		Galeopsis tetrahit		*Sambucus nigra*	
		Barbarea stricta		*Vicia sepium*	
		Cardamine impatiens		*Cuscuta europaea*	
		Chelidonium majus		*Scrophularia nodosa*	
		Festuca gigantea		*Carduus nutans*	
		Myosotis sylvatica		*Chelidonium majus*	
		Picris hieracioides		*Cruciata laevipes*	
		Stellaria nemorum			
		Verbascum nigrum			
	Swamp and alluvial forests	*Filipendula ulmaria*	37.3	*Filipendula ulmaria*	42.4
	(*Alnion-glutinosae, Alno-Ulmion*)	*Alnus glutinosa*		*Humulus lupulus*	
		Circaea lutetiana		*Phragmites australis*	
		Equisetum arvense		*Lycopus europaeus*	
		Lycopus europaeus		*Fraxinus excelsior*	
		Brachypodium sylvaticum		*Alnus glutinosa*	
		Acer psedoplatanus		*Hedera helix*	
		Clematis vitalba		*Salix triandra*	
		Fraxinus excelsior		*Acer campestre*	
		Quercus robur		*Corylus avellana*	
		Dryopteris filix-mas		*Dryopteris filix-mas*	
		Stachys sylvatica		*Equisetum arvense*	
		Acer campestre		*Lysimachia nummularia*	
		Carex acutiformis		*Ribes rubrum*	
		Festuca gigantea			

		Hedera helix *Ribes rubrum* *Salix aurita* *Stellaria nemorum*			
	Flooded meadows, grasslands on trampled ground (*Agrostietea stoloniferae, Plantaginetea majoris*)	*Equisetum arvense* *Taraxacum sect. Ruderalia* *Lolium perenne* *Festuca arundinacea* *Potentilla reptans* *Barbarea stricta* *Plantago major* *Potentilla anserina* *Trifolium repens* *Veronica serpyllifolia*	19.6	*Equisetum arvense* *Lysimachia nummularia* *Plantago major*	9.1
	Arable land, annual ruderal communities (*Chenopodietea*)	*Equisetum arvense* *Taraxacum sect. Ruderalia* *Bromus hordeaceus* *Galeopsis tetrahit* *Geranium molle* *Papaver rhoeas* *Stellaria media*	13.7	*Bromus arvensis* *Calamintha menthifolia* *Equisetum arvense*	9.1
	Bur-marigold and orache bank communities (*Bidentetea*)	-	0.0	-	0.0
Downstream	Nitrophilous tall herb communities (*Galio-Urticenea*)	*Scrophularia nodosa* *Solanum dulcamara* *Brassica nigra* *Cuscuta europaea* *Anthriscus sylvestris* *Linaria vulgaris* *Ballota nigra* *Cruciata laevipes* *Erysimum cheiranthoides* *Eupatorium cannabinum* *Hypericum hirsutum*	52.0	*Poa trivialis* *Rumex obtusifolius* *Ranunculus ficaria* *Symphytum officinale* *Angelica archangelica* *Nepeta cataria* *Tanacetum vulgare*	43.7

	Melilotus officinalis *Ranunculus ficaria*			
Swamp and alluvial forests (*Alnion-glutinosae, Alno-Ulmion*)	*Prunus padus* *Ranunculus ficaria* *Salix purpurea*	12.0	*Ranunculus ficaria* *Symphytum officinale* *Cirsium oleraceum*	18.8
Flooded meadows, grasslands on trampled ground (*Agrostietea stoloniferae, Plantaginetea majoris*)	*Juncus effusus*	4.0	*Poa trivialis* *Rumex obtusifolius* *Symphytum officinale* *Trifolium repens*	25.0
Arable land, annual ruderal communities (*Chenopodietea*)	*Chenopodium album* *Erysimum cheiranthoides* *Matricaria recutita* *Thlaspi arvense*	16.0	*Sonchus asper* *Fallopia convolvulus*	12.5
Bur-marigold and orache bank communities (*Bidentetea*)	*Persicaria lapathifolia* *Persicaria dubia* *Erysimum cheiranthoides*	16.0	-	0.0

Figure A3.1 - Site conditions upstream of the weir in Fürfurt (sampled in June 2017).

Figure A3.2 - Site conditions downstream of the weir in Fürfurt (sampled in June 2017).

Figure A3.3 - Hydrodynamic conditions at the weir crest in Fürfurt (sampled in June 2017).

Chapter 4

River regulation intensity matters: Riverbank vegetation is characterized by more typical riverbank plant species with growing distance to weirs – Results of field studies along the German river Lahn

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Abstract

Questions

We aim to assess the ecological value of weir-distant (1000 m minimum weir distance) and weir-near riverbank vegetation (upstream and downstream in a maximum weir distance of 400 m) in answering the following questions: (a) Is downstream species composition more similar to upstream or to weir-distant species composition; (b) are there differences in species diversity, functional diversity and species´ life strategies and (c) which site harbors more species from riverbank zones that are naturally governed by a high water level fluctuation level?

Location

River Lahn, Hesse, Rhineland-Palatinate, Central Germany.

Methods

We sampled 72 relevés along weir-distant (24 relevés) and weir-near reaches (upstream and downstream: 24 relevés each). Differences in species composition were evaluated by non-metric multidimensional scaling and indicator species analysis. We compared species diversity, functional diversity and csr-signatures to test for differences between upstream, downstream and weir-distant sites using a Kruskal-Wallis test by ranks and a Posthoc-Kruskal-Nemenyi-Test. Indicator species were used to analyze the distribution of typical species from the transition zone of riverbanks.

Results

Weir-distant vegetation was distinctly different from weir-near vegetation, revealing more relations to typical floodplain species and species adapted to flooding and changing water levels, a higher species diversity and a partly higher functional diversity. R-strategists were more present along the weir-distant reaches, which applies also to species from flooded meadows and grasslands. Summer annual species from the *Bidentetea* alliance were rare.

Conclusions

Uniform vegetation patterns due to river regulation can be reduced by lower river regulation intensity. As summer annual species were rare, we recommend to assess the ecological value of regulated riverbank stretches by means of species that occur naturally directly above the summer annual species zone. These species occurred irrespective of the weir distance and corresponded to water level fluctuation intensity.

4.1 Introduction

Recurring flooding events and water level fluctuations that vary in space and time are one of the major determinants for the characteristic zonation of riparian plant communities, naturally being harbored by a wide range of strongly adapted species (ELLENBERG & LEUSCHNER 2010; WARD 1998).

Regulation measures like river damming impede the river´s natural disturbance dynamics (POFF ET AL. 2007). Thus, the space for the establishment of a typical riparian zonation is restricted to a reduced space, leading to the establishment of novel assemblies of riparian plant communities (HARVOLK ET AL. 2014). These are less able to cope with flooding and consist mainly of nutrient and moisture demanding species from nitrophilous tall herb communities (*Galio-Urticenea*). Simultaneously, space for habitat types being subject to frequent disturbances by fluctuating water levels along riverbanks decreased significantly. This applies to reeds of flowing waters and flooded meadows and grasslands, but in particular, also to the riparian plant communities of the *Bidention tripartitae* and the *Chenopodion rubri* (FEDERAL AGENCY FOR NATURE CONSERVATION 2011), occurring during low water stages in summer below the shoreline´s mean and low water line (OBERDORFER 1993). These plant communities are classified as strongly endangered in Germany (FINCK ET AL. 2017), which also applies to other European rivers, as most of the undertaken regulation measures worldwide concentrate on them (NILSSON ET AL. 2005). Against this background, these habitat types are under the protection of the EU Habitats Directive (Council Directive 92/43/EEC, habitat type 3270: rivers with muddy banks with *Chenopodion rubri* p.p. and *Bidention* vegetation p.p.).

River damming is also a frequently distributed regulation measure along German Federal Waterways, amounting to two-thirds of the waterways network and ensuring their unimpeded use for shipping traffic (STAMM 2006). Smaller installations of impoundments like run-of-river impoundments or weirs are found along smaller waterways like the Hessian rivers Lahn and Fulda, where they are accompanied by lockages, ensuring barrier liberty for navigation. Weirs are characterized by permanent water flows over the weir crest through the whole year (CSIKI & RHOADS 2010), therefore ensuring at least a certain extent of flood seasonality downstream of weirs. Nonetheless, also these types of impoundments led to profound alterations of the natural disturbance regime, which is expressed by a reduction of flooding frequency and intensity (BUNN & ARTHINGTON 2002). As consequences for the biotic environment the inhibition of hydrochorous seed dispersal (ANDERSSON ET AL. 2000; MERRITT & WOHL 2006), declines in riparian species diversity (DYNESIUS ET AL. 2004) and alterations of riparian zonation (NEW & XIE 2008) are documented. By contrast to dams (FITZHUGH & VOGEL 2011; JOHNSON ET AL. 2012), the effects of weirs on riverbank vegetation gained less attention to date, although the weir installations date from the Middle Ages. As the European Water Framework Directive targets at least a good ecological potential along all European rivers until 2027 (THE EUROPEAN PARLIAMENT 2000), more attention should be devoted to this topic.

Therefore, we studied the effect of weirs on riverbank vegetation in a previous study (WOLLNY ET AL. 2019). We investigated, whether riverbanks in direct proximity to weirs provide remnant habitat for summer annual species from the *Bidentetea* alliance. For our study, we recorded riverbank vegetation along the right- and left-hand shoreline within a distance of 1000 m upstream and downstream of weirs along the Hessian rivers Lahn and Fulda. Nearly constant water levels, low water flow velocities and a significantly lower bank steepness than downstream were characteristic upstream. By contrast, significantly higher water level fluctuations, higher flow velocities and significantly steeper banks were dominant downstream, leading to wider transition zones than upstream. Our results revealed that species from reeds of still waters, swamp and alluvial forests and terrestrial habitats were representative for upstream reaches. Further, upstream species composition mainly consisted of c- and cs-strategists and perennials. Vice versa, species from reeds of flowing waters, flooded meadows and grasslands were indicative for the downstream reaches. *Bidentetea* species were rare and limited to areas with low bank inclination. Less competitive species with short life-spans occurred more frequently downstream. Against this background, we predict restoration measures along impounded rivers to be the most successful along sites with significantly higher levels of water level fluctuations and low bank inclinations by contrast to upstream sites. In our previous study, this applies to the downstream reaches.

As our study´s data basis was confined to river stretches in direct proximity to weirs that display high levels of regulation, we were not able to assess the relation of our results against the background of regulation intensity. For a regulation intensity-based assessment aiming at formulate appropriate riverbank restoration measures along regulated rivers, we sampled riverbank vegetation along the Lahn river stretch (Marburg to Lollar), where lockages in direct surroundings to the weirs are absent. Therefore, the impoundment effect is further minimized. Data sampling along this river stretch was restricted to areas in a minimum distance of 1 km to the next weir. The fluctuation of water levels along the weir-distant reaches is comparable to the downstream reaches. By contrast to our previous study, the present study aims to assess the relationship between vegetation in near proximity to weirs and riverbank vegetation in a larger distance to the next weir (hereafter: weir-distant). Overall, the following questions were of particular interest for our study:

1. Is downstream species composition more similar to upstream or to weir-distant species composition?
2. Are there differences in species diversity, functional diversity and species´ life strategies between weir-distant and weir-near reaches?
3. Which site harbors more species from riverbank zones that are naturally governed by a high water level fluctuation level?

4.2 Methods

4.2.1 Study area

Vegetation sampling was conducted north and south-west of the German city Giessen along the Lahn river middle course (Fig. 4.1; FEDERAL WATERWAYS AND SHIPPING ADMINISTRATION 2008).

Weir-distant relevés were sampled along 23 river-km upstream from Giessen between Marburg (177 m a.sl.) and Lollar (165 m a.sl.) along the Non-Federal-Waterway stretch during June 2018. Weir-near relevés were recorded from Dorlar (Federal-Waterway-km 3.2, 153 m a.s.l.) to Scheidt (Federal-Waterway-km 97.2, 100 m a.s.l.) during June, July and August of 2016 and 2017 covering 93 river-km of the Federal Waterway river stretch. To display the hydrologic conditions during the data sampling, we summarized the mean water discharges in Fig. 4.2. Except for Löhnberg, Fürfurt and Scheidt (river Lahn valley of Giessen and Koblenz), our study sites belong to the Western Hessian Mountainous and Sink Countries (KLAUSING 1988). Detailed information on climate, the geological understorey, dominating soil types, bank inclination, hydrological properties, abiotic and biotic environment and vegetation structure are summarized in Table 4.1.

The surrounding land use along the Non-Federal Waterway is mainly characterized by agriculture, whereas the share of grassland and forests increases between Dorlar and Scheidt. Weirs were constructed during the Middle Ages for reasons of milling activities (STATE OFFICE FOR WATER MANAGEMENT OF RHINELAND-PALATINATE 1997). Compared to the weirs between Marburg and Lollar, the ones along the river stretch being classified as Federal Waterway are accompanied by lockages.

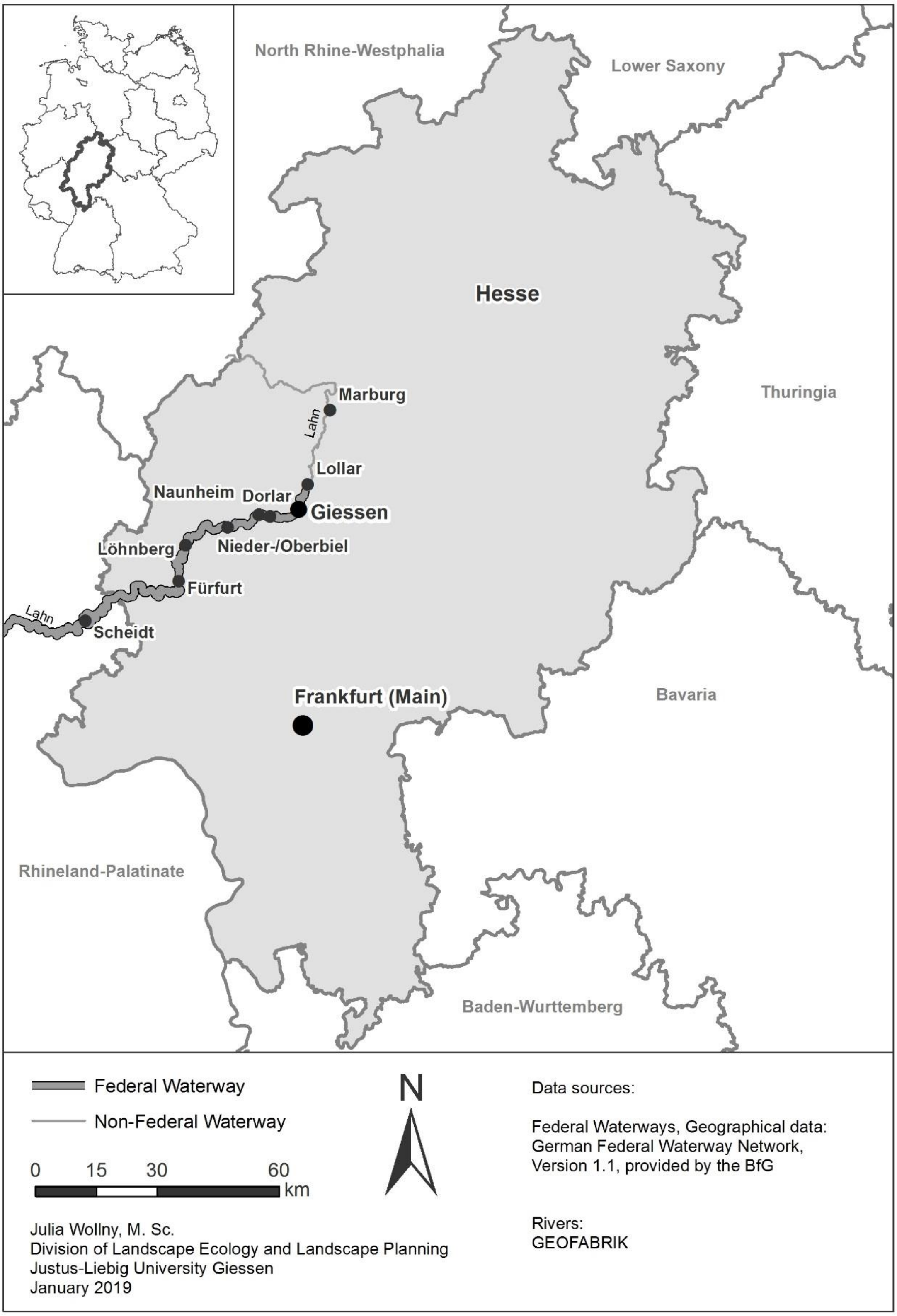

Fig. 4.1 - Study site location (Figure adapted to WOLLNY ET AL. (2019)).

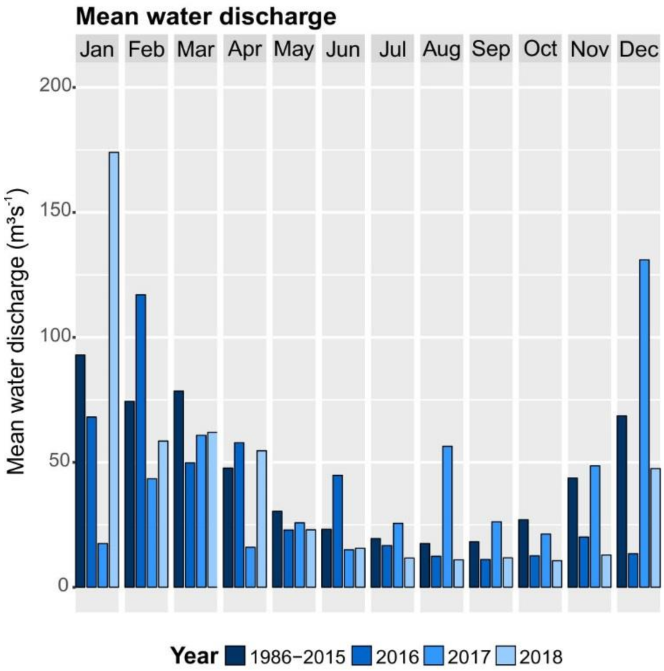

Fig. 4.2 - Long-term mean water discharges (1986-2015) and mean water discharges for the sampling years (2016-2018), measured at the water level monitoring station Kalkhofen (FEDERAL WATERWAYS AND SHIPPING ADMINISTRATION 2019).

Table 4.1 - Local site conditions along the Lahn (mean ± standard deviation), separated for weir-near (upstream, downstream) and weir-distant relevés. Mean water level fluctuation data for weir-near relevés were retrieved from 1D hydrological models implemented in FLYS 3.2.1, provided by the German Federal Institute for Hydrology. Hydrological data for weir-distant relevés originate from the water level monitoring station in Marburg and were provided by the Hessian State Office for Environment, Nature Conservation and Geology. Data on bank inclination, abiotic and biotic environment and vegetation structure were sampled in the field. Asterisks indicate statistical differences of the mean values (*p<0.05; **p<0.01; ***p<0.001), which were evaluated by a Kruskal-Wallis test by ranks (p<0.05). Same letters display homogenous groups, determined by a Posthoc-Kruskal-Nemenyi-Test (p<0.05). References: Climate: HESSIAN STATE OFFICE FOR ENVIRONMENT AND GEOLOGY (2013c); geological understorey: HESSIAN STATE OFFICE FOR ENVIRONMENT AND GEOLOGY (2013b); dominating soil types: Hessian State Office for Environment AND Geology (2013a); flow regime: KOENZEN (2005); mean water discharge (Federal Waterway; water level monitoring station Kalkhofen): FEDERAL WATERWAYS AND SHIPPING ADMINISTRATION (2008a), mean water discharge (Non-Federal Waterway; water level monitoring station Marburg): HESSIAN STATE OFFICE FOR ENVIRONMENT AND GEOLOGY (2010). Table adapted according to WOLLNY ET AL. (2019).

	Specification	**Upstream (weir-near) (n=24)**	**Downstream (weir-near) (n=24)**	**Weir-distant (n=24)**
Climate	Mean annual temperature (°C)	8-9	8-9	7-8
	Mean annual precipitation (mm)	600-700	600-700	700-800
Geological understorey	-	Holocene alluvial sediments	Holocene alluvial sediments	Holocene alluvial sediments
Dominating soil types	-	Vega, gley, pseudogley	Vega, gley, pseudogley	Vega, gley, pseudogley
Hydrological properties	Flow regime	Pluvial	Pluvial	Pluvial
	Mean water discharge (m^3 s^{-1})	49.5	49.5	16.3
	Mean water level (cm)	132.9 ± 19.4	130.1 ± 20.1	198.5 ± 7.9
	Mean water level fluctuation (m)***	1.4 ± 0.2 (a)	3.5 ± 1.1 (b)	3.8 ± 2.7 (b)
Bank inclination (%)* **	-	13.3 ± 6.5 (a)	33.7 ± 21.5 (b)	29.4 ± 26.0 (ab)
Abiotic environment	Relevés with open soil (n relevés)	4	2	24
	Coverage open soil (%)	8.75 ± 4.2	17.5 ± 12.5	25.6 ± 15.2
Biotic environment	Litter (n relevés)	5	5	24
	Coverage (%)	10.0 ± 5.5	12.0 ± 4.0	15.2 ± 11.2
Vegetation structure	Tree layer (n relevés)	14	8	23
	Coverage (%)*	47.1 ± 31.7 (a)	71.9 ± 27.0 (b)	39.1 ± 15.3 (a)
	Height (m)	11.8 ± 5.2	8.8 ± 3.6	10.7 ± 2.6
	Shrub layer (n relevés)	10	6	11
	Coverage (%)*	27.5 ± 30.7 (ab)	39.2 ± 12.0 (a)	13.3 ± 10.5 (b)
	Height (m)	3.0 ± 1.1	4.0 ± 1.3	3.8 ± 1.5

4.2.2 Study design and vegetation sampling

To represent weir-near vegetation, we used vegetation relevés that were recorded in 400 m and 200 m distance to each weir upstream and downstream on the right and left-hand bank side from our previous study (Fig. 4.3; WOLLNY ET AL. 2019). As direct effects of weirs are expected to be most evident within a distance up to 1000 m to the weir (J. SCHMIDT, Federal Waterways and Shipping Administration, personal communication, January 31, 2017), weir-distant vegetation was sampled randomly in a minimum distance of 1000 m to the weirs. Upstream, downstream and weir-distant vegetation is represented by 24 relevés each, resulting in 72 relevés in total.

Riverbank vegetation was sampled in relevés of 10 m length along and 2 m width vertical to the shoreline (DYNESIUS ET AL. 2004), starting directly above the actual-water-level-line. We used the modified Braun-Blanquet numerical scale for the estimation of species abundances (VAN DER MAAREL 1979) and used the nomenclature of JÄGER (2013) for species identification.

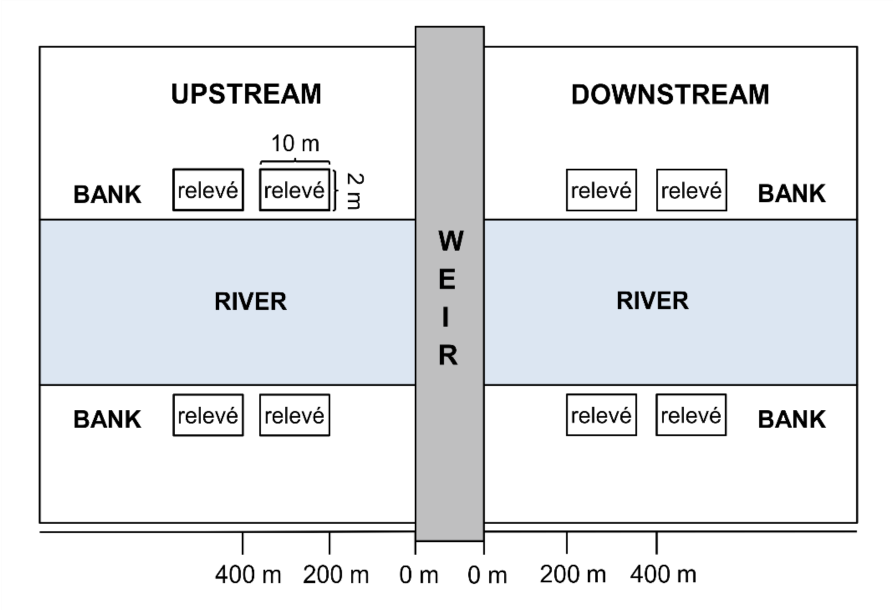

Fig. 4.3 - Sampling design for weir-near vegetation (adapted to WOLLNY ET AL. (2019)).

4.2.3 Statistical analyses

Non-metric multidimensional scaling (NMS) was used to reveal differences in species composition between weir-near and weir-distant riverbank vegetation and the most important environmental gradients (Table 4.2). Sørensen distances display similarities among relevés (Bray-Curtis distance). 200 iterations, three dimensions and a random starting configuration were chosen as initial settings for our analysis. To account for rare species, percentage values of species abundances were transformed via square root transformation prior to the ordination in PC-ORD 7 (McCune & Mefford 2016).

Similarities in species composition were evaluated by indicator species analysis (Dufrêne & Legendre 1997), detecting significant indicator species for each reach and for study reach combinations (Cáceres et al. 2010). Significant indicator species were specified by an indicator value >25 and a p-value <0.05 (Dufrêne & Legendre 1997) and were detected by the R-package *indicspecies* (Cáceres & Legendre 2009) in R 3.4.4 (R Development Core Team 2018).

We analyzed species diversity using the species diversity measures Richness, Shannon index (Shannon & Weaver 1963) and Evenness (Hill 1973) that were calculated in Turboveg 2.127 (Hennekens & Schaminée 2001).

To evaluate functional diversity, we calculated functional richness, functional evenness (Mason et al. 2005), functional divergence (Villéger et al. 2008) and functional dispersion (Laliberté & Legendre 2010) by means of the R-package *FD* (Laliberté & Legendre 2010) in R 3.4.4 (R Development Core Team 2018). The ecological and trait values used for the measures´ calculation (Appendix S1) were extracted from the Ellenberg indicator values (Ellenberg et al. 1991) and the BiolFlor (Kühn et al. 2004) and LEDA (Kleyer et al. 2008) databases.

Due to lacking requirements for parametric tests, a Kruskal-Wallis test by ranks was used for the validation of statistical differences in R 3.4.4 (R Development Core Team 2018). Homogenous groups were determined using a Posthoc-Kruskal-Nemenyi-Test implemented in the R-package *PMCMRplus* (Pohlert 2018). Statistical differences for Richness, s- and r-signature (explained in chapter 2.4) were tested using ANOVA, as these variables fulfilled the requirements for parametric tests. The corresponding homogenous groups were determined by a pairwise t-test including Holm correction.

Table 4.2 - Environmental variables used for NMS.

Category	Variable	Abbreviation	Unit
Topography	Altitude	Altitude	m
	Bank inclination	Inclin	%
Vegetation	Cover tree layer	Cov_tree	%
	Cover shrub layer	Cov_shrub	%
	Cover herb layer	Cov_herbs	%
	Cover grass layer	Cov_grass	%
	Cover litter layer	Cov_litter	%
	Cover open soil	Cov_soil	%
Species diversity	Richness	Richness	Unitless
	Shannon index	Shannon	Unitless
	Evenness	Evenness	Unitless
Functional signature	C-signature	C-signature	Unitless (range of values: 0-1)
	S-signature	S-signature	Unitless (range of values: 0-1)
	R-signature	R-signature	Unitless (range of values: 0-1)
Local site conditions	Mean Ellenberg indicator value (light)	EIV Light	Unitless
	Mean Ellenberg indicator value (moisture)	EIV Moisture	Unitless
	Mean Ellenberg indicator value (reaction)	EIV Reaction	Unitless
	Mean Ellenberg indicator value (nutrient)	EIV Nutrient	Unitless

4.2.4 C-S-R signatures and species habitat origin

We determined c-s-r signatures for each relevé according to HUNT ET AL. (2004) to display the response of the whole plant community towards the hydrodynamic environment.

To reveal detailed differences in species composition, we analyzed species´ habitat origin, using significant and not significant indicator species (Appendix S3) and excluding stand-forming species like *Urtica dioica* and *Impatiens glandulifera* (Appendix S4) from our analysis. Related information for each species was retrieved from FloraWeb, a website that provides a broad information pool for wild plants in Germany and which is maintained by the German Federal Agency for Nature Conservation. Due to limited availability of species data being classified as *major occurrences*, we collected all available species information that were categorized as *main occurrences*, which were listed under the heading "Formation" (KORNECK ET AL. 1998), displaying regular occurrences of species in habitats (FEDERAL AGENCY FOR NATURE CONSERVATION 2019). The following habitats were of importance for our analysis: Nitrophilous tall herb communities (*Galio-Urticenea*) to reflect the regulation level; swamp and alluvial forests (*Alnion-glutinosae, Alno-Ulmion*) to display low water flow velocities; wet grassland (*Molinietalia caeruleae*) and mesophilic grassland (*Arrhenatherion elatioris*) to illustrate terrestrialization tendencies; flooded meadows and grasslands on trampled ground (*Agrostietea stoloniferae, Plantaginetea majoris*) to display recurring flooding events; bur-marigold and orache communities (*Bidentetea*) to reflect water level fluctuations; arable land and annual ruderal communities (*Chenopodietea*) indicating recurring disturbance events.

4.3 Results

4.3.1 Species composition

The whole dataset comprised 194 species, whereby the most frequent across all relevés were *Urtica dioica* (97%), *Impatiens glandulifera* (82%) and *Galium aparine* (65%). The highest number of species restricted to one reach was observed along the weir-distant relevés (53 species), whereas 28 species occurred just upstream. Ten species were limited to downstream reaches. Upstream and weir-distant reaches had the highest number of common species (27). By contrast, downstream and weir-distant reaches had 13 species in common. 11 species were limited to the weir-near reaches (Appendix S5).

The ordination revealed a clear separation of the relevés according to the distance to the weir by axis one (Fig. 4.4). Weir-near relevés were associated with higher levels of moisture and nutrients, revealed by the vectors of EIV Moisture (r^2=0.243) and EIV Nutrient (r^2=0.467). Furthermore, species composition was correlated with a higher c-signature (r^2=0.492). By contrast, weir-distant relevés indicate higher species diversity, being displayed by the vectors for Shannon index (r^2=0.634), Richness (r^2=0.541) and Evenness (r^2=0.401). Unlike upstream and downstream species composition, weir-distant vegetation showed higher s- and r-signatures ($r^2_{s\text{-signature}}$=0.330; $r^2_{r\text{-signature}}$=0.274) and a higher proportion of open soil recorded in the relevés (r^2=0.272). Although the river stretch of the weir-distant relevés was much shorter (23 km) than the river stretch of the weir-near relevés (93 km), ordination space occupied by the weir-distant relevés is comparable to the weir-near relevés. Bank inclination (r^2_{Inclin}=0.048; axis 3) and soil conditions ($r^2_{EIV\ Reaction}$=0.073; axis 2) were of small importance for data variation.

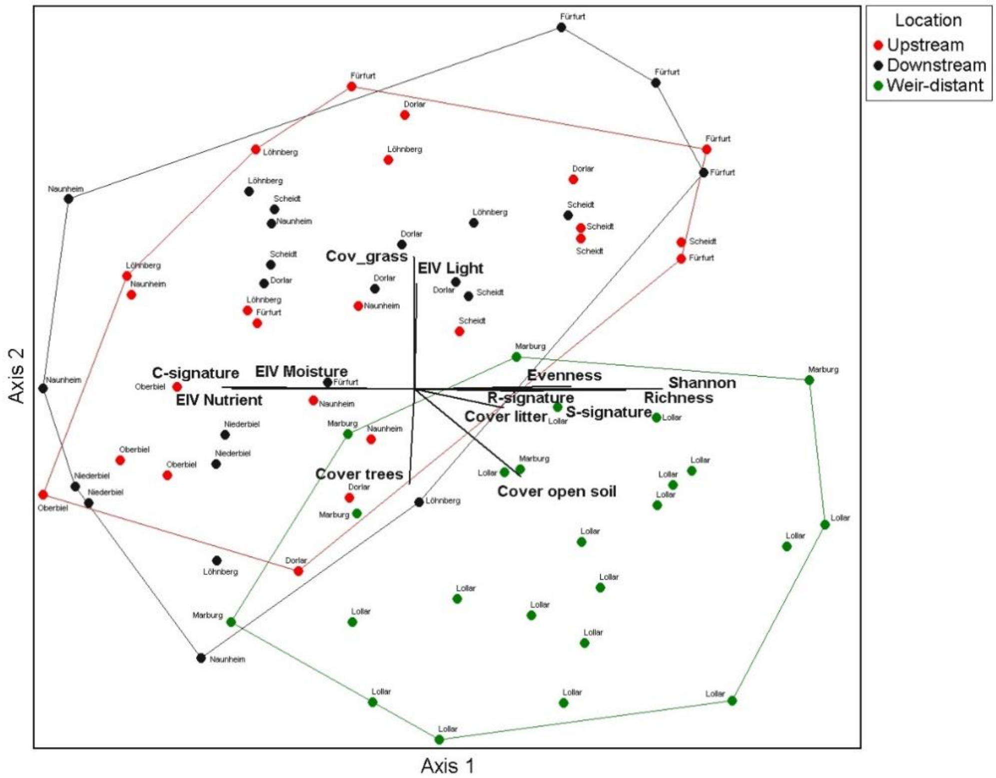

Fig. 4.4 - Ordination plot of the final three-dimensional non-metric multidimensional scaling (NMS) for the Lahn vegetation data. One point represents one relevé. The relevé arrangement was built by means of Bray-Curtis dissimilarities. Final stress amounts to 19.41 and 65.5% of the total variance is explained by axis 1 (r^2=0.294), axis 2 (r^2=0.206) and axis 3 (r^2=0.154). Environmental variables r^2<0.2 are not shown. Correlations of the environmental variables with ordination axes are summarized in Appendix S2.

Indicator species analysis determined the highest number of significant indicator species for the weir-distant reaches (Table 4.3). Weir-distant indicator species show adaptations to fluctuating water levels (indicated by ~) and flooding (indicated by =). These species were absent along the weir-near reaches. Indicator species following cs-strategy were common upstream, whereas c-strategists were dominant along the weir-distant reaches. R- and s-strategists were absent across all reaches. Common indicator species were restricted to the combination of upstream and weir-distant reaches, being mostly c-strategists. A weir-distance related pattern of the Ellenberg indicator values for moisture was not detectable.

Table 4.3 - Significant indicator species for upstream (U, n=24), downstream (D, n=24) and weir-distant (W, n=24) vegetation. Each indicator species is specified by indicator value (IV), p-value, Ellenberg indicator value (EIV) for moisture (ELLENBERG ET AL. 1991) and life strategy after GRIME (1979). High levels of the Ellenberg indicator value indicate a higher demand for moisture than species with medium and low levels. Indicator species characterized by an x (indifferent behaviour) exhibit a wide ecological amplitude towards moisture, ~ indicates adaptations to water level fluctuations and = adaptations to flooding. Life-strategies after GRIME (1979): c=competitors, r=ruderal, s=stress tolerators and combinations thereof.

Reach	Indicator species	IV	p-value	EIV moisture	Life strategy
U	*Lamium maculatum*	0.701	0.001***	6	csr
	Phragmites australis	0.676	0.001***	10	cs
	Stellaria graminea	0.456	0.006**	5	cs
	Rumex sanguineus	0.405	0.047*	8	cs
D	*Vicia cracca*	0.411	0.04*	6	c
W	*Silene dioica*	0.743	0.001***	6	c
	Elymus caninus	0.675	0.001***	6	c
	Acer campestre	0.577	0.001***	5	c
	Fraxinus excelsior	0.533	0.002**	x	c
	Arctium lappa	0.556	0.003**	5	c
	Euonymus europaeus	0.477	0.007**	5	c
	Festuca gigantea	0.456	0.009**	7	cs
	Galium palustre	0.456	0.011*	9=	cs
	Veronica beccabunga	0.408	0.025*	10	cs
	Anthriscus sylvestris	0.451	0.030*	5	c
	Lysimachia nummularia	0.408	0.033*	6~	csr
	Barbarea vulgaris	0.400	0.042*	6	cr
U+D	-	-	-	-	-
U+W	*Aegopodium podagraria*	0.741	0.005**	6	c
	Filipendula ulmaria	0.740	0.007**	8	c
	Alnus glutinosa	0.593	0.018*	9=	c
	Equisetum arvense	0.479	0.035*	6~	cr
D+W	-	-	-	-	-

Species composition was mostly dominated by species from nitrophilous tall herb communities followed by species from swamp and alluvial forests, wetland and mesophilic meadows (Fig. 4.5).

Proportions of species from nitrophilous tall herb communities were highest downstream. By contrast, species from swamp and alluvial forests were absent downstream and restricted to upstream and weir-distant sites, whereby the proportion was higher along the weir-distant reaches. Levels of wetland and mesophilic meadow species were nearly balanced and highest upstream. Compared to mesophilic meadow species, wetland meadow species are of minor importance along the weir-distant reaches. Species from flooded meadows occurred in medium levels and reached the highest proportions along weir-distant reaches, whereas the lowest proportions were observable upstream. By contrast, species from bur-marigold and orache bank communities were generally rare and limited to weir-distant reaches. Species originating from arable land and annual ruderal communities played a minor role for species composition and reached the highest proportions weir-distant, whereas these species were absent downstream.

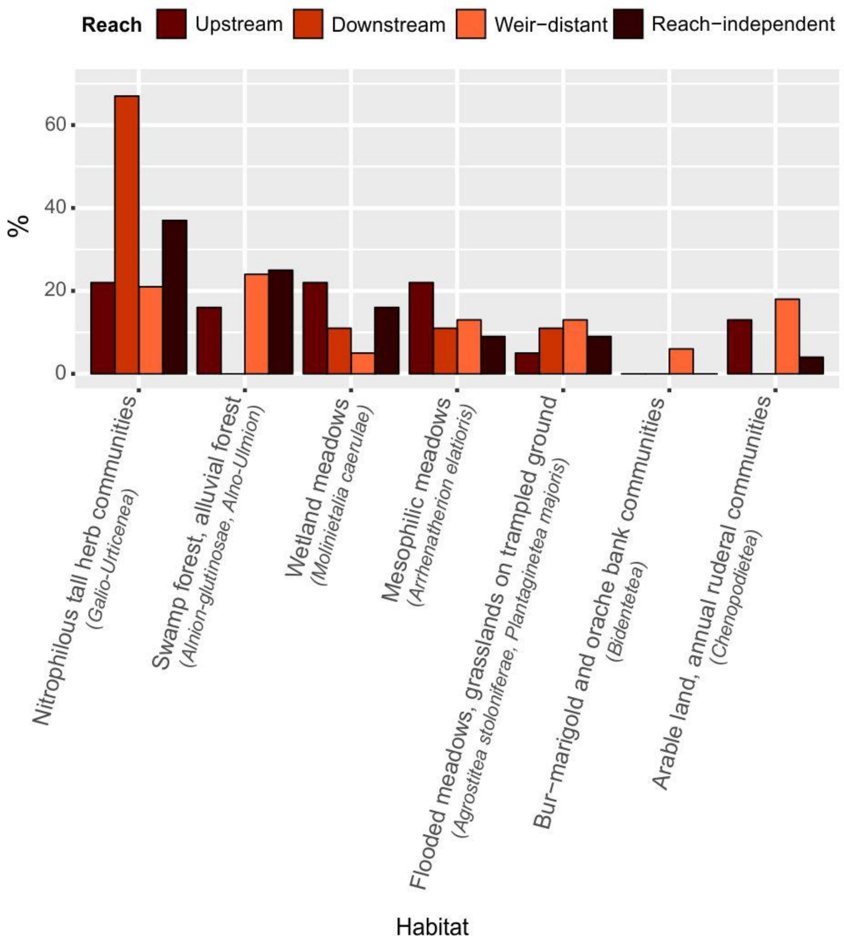

Fig. 4.5 - Habitat binding of indicator species for upstream, downstream and weir-distant reaches and reach-independent species indicated by bars displaying percentage values. Appendix S6 contains detailed information on species´ identity. Data for relevant habitats (multiple answers possible) retrieved from FloraWeb (KORNECK ET AL. 1998a). Figure adapted according to WOLLNY ET AL. (2019).

4.3.2 Species´ ecological and functional traits

The lowest c-signature (Fig. 4.6a) was observed for species composition along the weir-distant reaches, whereas downstream values were significantly higher. Upstream values were lower than downstream but higher than along the weir-distant reaches. Statistical differences to downstream and to weir-distant reaches were nonexistent. S-signatures were also not significantly different across the reaches, but tended to increase from upstream to downstream and from downstream to weir-distant reaches (Fig. 4.6b). With exception of the downstream reaches, this trend was also true for the r-signatures along upstream and weir-distant reaches (Fig. 4.6c). The lowest r-signatures were observed for the downstream reaches, showing significant differences to weir-distant reaches.

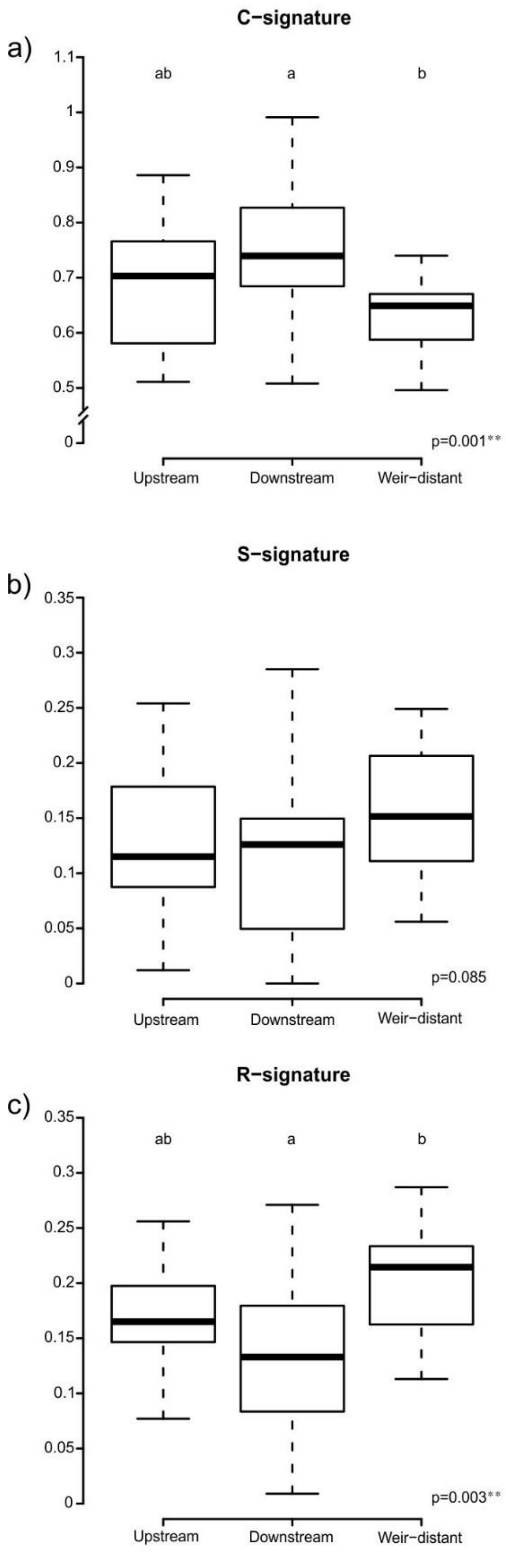

Fig. 4.6 - Results of the statistical comparison of c-, s-, and r-signatures of riverbank species along upstream (n=24), downstream (n=24) and weir-distant (n=24) reaches. Same letters indicate homogenous groups. Levels of significance: *$p<0.05$; **$p<0.01$; ***$p<0.001$.

4.3.3 Diversity and functional diversity

All species diversity indices offer a clear pattern, revealing a significantly higher mean species diversity in weir-distant relevés (Table 4.4). When directly comparing upstream and downstream relevés, mean values of Richness and Shannon-Diversity tended to be lower downstream, whereas Evenness tended to higher levels.

Similar to species diversity, also functional richness and functional evenness were significantly higher along the weir-distant reaches. Whereas functional richness was the lowest along the downstream reaches, mean functional evenness values displayed hardly any differences between upstream and downstream reaches. Levels of functional divergence and functional dispersion were not different between study reaches.

Table 4.4 - Results of the statistical comparison of diversity and functional diversity measures (mean ± standard deviation) for weir-distant (n=24), upstream (n=24) and downstream reaches (n=24). Different letters imply statistical differences. Levels of significance: *p<0.05; **p<0.01; ***p<0.001.

	Measure	**Upstream (n=24)**	**Downstream (n=24)**	**Weir-distant (n=24)**
Diversity	Richness ***	20.0 ± 8.2 (a)	16.2 ± 6.5 (a)	25.7 ± 5.3 (b)
	Shannon index ***	2.3 ± 0.5 (a)	2.1 ± 0.5 (a)	2.8 ± 0.3 (b)
	Evenness *	0.8 ± 0.1 (a)	0.8 ± 0.1 (a)	0.9 ± 0.1 (b)
Functional Diversity	Functional Richness ***	0.10 ± 0.09 (a)	0.06 ± 0.05 (a)	0.15 ± 0.07 (b)
	Functional Evenness **	0.70 ± 0.08 (a)	0.67 ± 0.12 (a)	0.76 ± 0.05 (b)
	Functional Divergence	0.77 ± 0.09	0.76 ± 0.09	0.79 ± 0.05
	Functional Dispersion	0.22 ± 0.05	0.23 ± 0.05	0.23 ± 0.03

4.4 Discussion

4.4.1 Essential differences in weir-near and weir-distant riverbank species composition

Results of the NMS revealed a clear separation between weir-distant and weir-near reaches, implying that upstream and downstream vegetation share more similarities in species composition than downstream and weir-near vegetation. Indicator species analysis confirmed this finding, as common indicator species for downstream and weir-distant reaches remained absent. Although similarities between weir-distant and weir-near sites were generally low, certain similarities were proven for upstream and weir-distant sites, sharing species like *Filipendula ulmaria* and *Aegopodium podagraria*. These belong to the nitrophilous tall herb communities that experienced an enormous spread in the last decades (OBERDORFER 1993), also due to river regulation, thus displaying river regulation irrespective of the distance to the weir well.

Nonetheless, by contrast to weir-near sites, weir-distant riverbank vegetation was related to higher habitat dynamics. This is reflected by the significant indicator species *Galium palustre* and

Lysimachia nummularia, which are adapted to changing water levels (indicated by ~) and to flooding (indicated by =) (ELLENBERG ET AL. 1991). Additionally, indicator species like *Veronica beccabunga*, *Festuca gigantea* and *Euonymus europaeus* demonstrate that weir-distant reaches show stronger relations to typical floodplain vegetation (OBERDORFER 1992b; OBERDORFER 1993). By contrast to the weir-distant sites, upstream and downstream sites were characterized by less significant indicator species, harboring grassland species like *Vicia cracca* and *Stellaria graminea*, that occur naturally far from rivers (OBERDORFER 1993), implying reduced habitat dynamics. This finding is strengthened by significantly higher occurrences of *Phragmites australis*, highlighting that especially the upstream reaches are subject to reduced habitat dynamics.

Due to similarities in water level fluctuation and bank inclination along downstream and weir-distant sites, we expected also analogies in riverbank species composition, as the riverine disturbance regime strongly determines riparian vegetation (TOCKNER & STANFORD 2002). Since factors like geology and climate are known to be further relevant for the variation in species composition (NILSSON & BERGGREN 2000), we took care to select weir-distant reaches being similar to the weir-near reaches in those aspects. Thus, these factors are not likely to cause the observed differences in species composition. By contrast, effects related to the natural environment are likely to be present, as relevés in the NMS were roughly arranged according to their location along the river. This is expectable, as riverine species composition is subject to longitudinal changes (WARD 1998).

However, weir-near relevés also reflect more occurrences of moisture and nutrient demanding species than weir-distant relevés. This is indicated by the gradients displaying the relevé´s mean Ellenberg indicator values for moisture and nutrients in the NMS. Weirs accompanied by lockages account for a relative increase of the water level (STATE OFFICE FOR WATER MANAGEMENT OF RHINELAND-PALATINATE 1997), which inducts essential shifts in the river´s flow regime and thus in nutrient cycling (NILSSON & BERGGREN 2000). Therefore, river regulation is also likely to account for differences in species composition between weir-near and weir-distant vegetation. River impoundments are proven to contribute to a higher importance of adjacent ecosystems for riverbank species composition as a consequence of dampened riverine hydrodynamics (JANSSON ET AL. 2000). As this applies especially to the reaches in direct weir proximity, this is also an argument for the observed differences in species composition due to river regulation intensity. Finally, it is worth mentioning that the ordination space occupied by weir-distant relevés is comparable to the weir-near relevés, although the recorded river stretch covers only a distance of 23 km (weir-near: 93 km). This implies a profoundly reduced species variation along the intensively regulated weir-near reaches, suggesting that the simple presence of water level fluctuations downstream does not guarantee a high variation in riverine species composition, which is typical for areas being exposed to recurring flooding events (TOCKNER & STANFORD 2002). The restoration of water level fluctuations is an often recommended measure (LEYER 2005; VAN GEEST ET AL. 2005), targeting the achievement of a more natural state along regulated rivers. With respect to river restoration measure planning, our findings on the effect of water level fluctuations underline the importance of the consideration of additional factors like the regulation intensity for the quality of river restoration measures.

4.4.2 Higher species diversity, functional diversity and improved adaptations of weir-distant plant species

The comparison of species diversity levels revealed a consistently and significantly higher species diversity along the weir-distant reaches. Further, species variation along these river stretches was higher. High species diversity is often associated with a high ecological value of ecosystems, which is true for the integrated assessment of floodplain ecosystems (NAIMAN ET AL. 1993). However, species diversity levels measured for our study present only a small part of the floodplain ecosystem. Thus, assessing the ecological value of weir-distant reaches just by means of species diversity is difficult. Therefore, we considered information on species identity by calculating functional diversity indices and csr-signatures. These are highly suitable to display predominant environmental processes and thus to reflect species´ adaptation to hydrodynamic disturbance events (BEJARANO ET AL. 2018). As riparian species composition along regulated rivers shifted to higher abundances of generalists and lower abundances of specialists (HARVOLK ET AL. 2014), this approach provides the opportunity to assess, whether high species diversity interacts with species adaptation and thus with a higher ecological value.

The lowest c-signatures were observed for the weir-distant reaches, whereas r- and s-signature reached the highest levels. These results point to higher species adaptation to stress and recurring disturbance events and thus to less competition between species (GRIME 1979). As the riverbank vegetation of unregulated rivers is characterized by many species exhibiting r- and cr-strategy (OBERDORFER 1993), this finding implies a lower regulation level along weir-distant reaches. C- and r-signatures of species downstream and weir-distant species were significantly different, again highlighting that species´ life strategies differ profoundly, although both sites share similarities in site conditions.

The observed patterns in species´ functional responses regarding river regulation are also apparent in functional diversity. Functional richness and functional evenness were significantly higher along the weir-distant reaches, whereas levels of functional divergence and functional dispersion were nearly equal. Missing differences in functional divergence and functional dispersion imply high similarities in species traits between upstream, downstream and weir-distant reaches

(VILLÉGER ET AL. 2008; LALIBERTÉ & LEGENDRE 2010). Thus, it can be concluded that all river stretches are affected by river regulation, which promotes uniform vegetation stands (WALSH ET AL. 2005). This finding is also supported by missing significances between weir-distant and upstream reaches regarding c- and r-signature. As species with higher adaptations to recurring disturbance events were reduced in abundance and frequency in the course of river regulation, equal levels in functional divergence and functional dispersion are transparent. However, it is possible that species with adaptations to recurring disturbance events remain underrepresented, although they occur in the dataset. Therefore, it is worth it to consider also functional diversity measures like functional richness, where species abundances remain unconsidered (VILLÉGER ET AL. 2008). Significantly higher levels of functional richness along the weir-distant reaches imply a larger occupied functional space, indicating a larger variation in species traits and thus the presence of more species exhibiting different traits. This finding is supported by a significantly higher functional evenness, implying a higher niche occupation along weir-distant sites and thus a more effective resource usage (MASON ET AL. 2005), although a significantly higher trait differentiation, reflected by functional divergence and functional dispersion, was not measurable.

Despite measurable regulation effects on riverbank vegetation both along weir-near and weir-distant reaches, our results regarding csr-signatures and functional diversity point to higher adaptations of species along weir-distant reaches and thus to a higher ecological value.

4.4.3 More species from riverbank zones that are naturally governed by frequent water level fluctuations along weir-distant reaches

A higher adaptation of weir-distant riverbank vegetation to fluctuating water levels was also indicated by our results of species´ habitat origin. Species occurrences from the summer annual *Bidentetea* communities like *Chenopodium polyspermum* and *Erysimum cheiranthoides* were limited to weir-distant reaches. These species are in decline due to reduced water level fluctuations because of river regulation (FEDERAL AGENCY FOR NATURE CONSERVATION 2011). Thus, their occurrences along the weir-distant reaches can be evaluated as positive for the ecological assessment of the weir-distant reaches. However, it is necessary to consider also the weather conditions for this assessment, as the occurrence of these species is highly dependent on low water levels during summer time, promoting open soil patches as essential requirements (ELLENBERG & LEUSCHNER 2010). Due to relatively higher mean water discharges that were mainly present during the field work in June 2016 but also in the second half of the year 2017, it is likely that these species were absent along the weir-near sites. By contrast, a strong heat and drought governed weather conditions in summer 2018, which resulted in extremely low water discharges and water levels until almost the end of the year, thus providing optimal conditions for the development of these species. Therefore, it is likely that the findings were more related to the weather conditions than to regulation intensity.

However, *Bidentetea* species were generally rare in our dataset. This might be due to the high bank steepness, which applies especially to the downstream and weir-distant sites, leading to weaker habitat dynamics than under natural conditions. In our previous study, occurrences of summer annual species were restricted to downstream reaches that exhibited low bank inclinations (WOLLNY ET AL. 2019). As the Lahn´s riverbanks are generally characterized by steep banks, it is likely that *Bidentetea* populations declined as a consequence and that current populations might be generally too small for frequent occurrences along the study sites. Another important reason for the rareness of summer annual species might be the strongly hampered transport of seeds and thus a reduced longitudinal connectivity between populations due to impoundments (ANDERSSON ET AL. 2000), which is an essential requirement for the survival of riverine plant populations (NILSSON & SVEDMARK 2002).

By contrast to summer annual species, species from flooded meadows and grasslands like *Potentilla reptans* and *Cardamine parviflora* were observed more often, indicating that these communities are more resistant towards river regulation. Compared to the *Bidentetea* species, they occur naturally above the *Bidentetea* species zone, but also in the transition zone of riverbanks, thus corresponding to fluctuating water levels (OBERDORFER 1993). Due to this, but also due to the presence both along weir-near and weir-distant habitats, these species are more applicable for the ecological assessment of riverbank habitats along regulated rivers than summer annual species, also, as they corresponded positively to the higher habitat dynamics along downstream and weir-distant reaches. As species from flooded meadows and grasslands were most common along weir-distant sites, these sites are related to a higher ecological value than the weir-near sites.

4.5 Conclusions

Overall, our results show that all river stretches are subject to river regulation. A high level of regulation intensity accounts to a major part for reduced levels of species diversity and partly of functional diversity. Moreover, competitive relationships are shifted, which disadvantages typical riverbank species. Vice versa, our study also illustrates that the level of regulation intensity provides good potential for the ecological enhancement of regulated rivers. This can be attained by reducing riverbank steepness and the removal of bank revetments like ripraps to increase habitat dynamics. Where possible, the removal of lockages in direct proximity to weirs can help to reduce the impoundment effect and thus to improve longitudinal connectivity. By this, riverbank vegetation can be enhanced by more typical riverbank species, leading to a higher ecological potential, which is claimed by the European Water Framework Directive.

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Appendix Chapter 4

Appendix S1 - Overview of the traits being the basis for the calculation of functional diversity indices, their abbreviation, data origin, scale level and trait specification. Binary data were signed with 1 if the specific trait applies to the species.

Trait	Abbreviation	Data origin	Scale	Specification
Guild	LifeForm	BiolFlor	Categorical	Woody (W) Herbaceous (H) Grass (G) Sourgrass (S) Legume (L)
Maximum height	CanHeight	LEDA	Numerical	meter (m)
Life span	LifeSpan_annual	BiolFlor	Binary	Annuals (one flowering phase)
	LifeSpan_perenn	BiolFlor	Binary	Perennials (more than one flowering phase)
Position of regenerative organ	Regeneration	Ellenberg	Categorical	Aboveground (a) Belowground (b) Therophyte (T)
Ecological optimum for moisture	EIV_moisture	Ellenberg	Categorical	Values between 1 and 10 (1 = dry site conditions to 10 = aquatic plants)
Tolerance for periodic wetness	Periodic_wet	Ellenberg	Binary	Ellenberg Indicator value – additional humidity value for periodic wetness
Flooding tolerance	Flooding	Ellenberg	Binary	Ellenberg Indicator value – additional humidity value for flooding

Appendix S2 - Correlations with ordination axes of the environmental variables used for NMS.

Environmental variable	Axis 1 R^2	Axis 2 R^2	Axis 3 R^2
Altitude	0.015	0.195	0.000
Inclin	0.000	0.002	0.048
Cov_tree	0.013	0.243	0.026
Cov_shrub	0.055	0.048	0.002
Cov_herb	0.157	0.007	0.008
Cov_grass	0.003	0.338	0.051
Cov_litter	0.229	0.049	0.003
Cov_soil	0.272	0.225	0.003
EIV Light	0.006	0.271	0.134
EIV Moisture	0.243	0.004	0.020
EIV Reaction	0.002	0.073	0.006
EIV Nutrient	0.467	0.000	0.001
Richness	0.541	0.005	0.020
Shannon	0.634	0.000	0.002
Evenness	0.401	0.009	0.011
C	0.492	0.006	0.059
S	0.330	0.006	0.011
R	0.274	0.001	0.069

Appendix S3 - Indicator species for upstream (U), downstream (D) and weir-distant (W) reaches and the respective combinations of reaches (U+D = upstream and downstream, U+W = upstream and weir-distant, D+W = downstream and weir-distant), with values for specificity and sensitivity, p-values and indicator values (IV). Significant indicator species exhibit an indicator value (IV) >25 and a p-value <0.05 (Monte Carlo randomization test).

Reach	Species name	A (Specificity)	B (Sensitivity)	IV	p.value	Significance
U	*Lamium maculatum*	0.6946	0.7083	0.7	0.000	***
	Phragmites australis	0.7835	0.5833	0.68	0.000	***
	Stellaria graminea	1	0.2083	0.46	0.0.	**
	Rumex sanguineus	0.7857	0.2083	0.41	0.05	*
	Rubus vulgaris	0.875	0.1667	0.38	0.1	.
	Prunus avium	1	0.125	.035	0.1	.
	Ranunculus repens	0.7353	0.2083	0.39	0.16	
	Calystegia silvatica	1	0.0833	0.29	0.29	
	Valeriana procurrens	1	0.0833	0.29	0.29	
	Holcus lanatus	1	0.0833	0.29	0.31	
	Bromus hordeaceus	1	0.0833	0.29	0.34	
	Valeriana versifolia	1	0.0833	0.29	0.35	
	Stellaria aquatica	0.7222	0.125	0.3	0.5	
	Vicia sepium	0.75	0.0833	0.25	0.75	
	Achillea millefolium	1	0.0417	0.2	1	
	Agrostis stolonifera	1	0.0417	0.2	1	
	Cardamine impatiens	1	0.0417	0.2	1	
	Chaerophyllum temulum	1	0.0417	0.2	1	
	Cirsium oleraceum	1	0.0417	0.2	1	
	Clematis vitalba	1	0.0417	0.2	1	
	Cornus sanguinea	1	0.0417	0.2	1	
	Fagus sylvatica	1	0.0417	0.2	1	
	Fallopia convolvulus	1	0.0417	0.2	1	
	Geranium molle	1	0.0417	0.2	1	
	Myosotis sylvatica	1	0.0417	0.2	1	
	Origanum vulgare	1	0.0417	0.2	1	
	Papaver rhoeas	1	0.0417	0.2	1	
	Picris hieracoides	1	0.0417	0.2	1	
	Plantago lanceolata	1	0.0417	0.2	1	
	Potentilla anserina	1	0.0417	0.2	1	
	Ribes rubrum	1	0.0417	0.2	1	
	Rumex acetosa	1	0.0417	0.2	1	
	Sorbus aucuparia	1	0.0417	0.2	1	
	Trifolium pratense	1	0.0417	0.2	1	
D	*Vicia cracca*	0.8125	0.2083	0.41	0.04	*
	Cuscuta europaea	0.8125	0.125	0.32	0.24	
	Brassica nigra	1	0.0833	0.29	0.32	
	Linaria vulgaris	1	0.0833	0.29	0.33	
	Solanum dulcamara	0.8571	0.0833	0.27	0.33	
	Helianthus tuberosus	1	0.0833	0.29	0.36	
	Rorippa amphibia	0.6154	0.125	0.28	0.52	
	Cruciata laevipes	1	0.0417	0.2	1	
	Epilobium ciliatum	1	0.0417	0.2	1	
	Epilobium obscurum	1	0.0417	0.2	1	
	Epilobium palustre	1	0.0417	0.2	1	
	Hypericum hirsutum	1	0.0417	0.2	1	
	Quercus petraea	1	0.0417	0.2	1	
	Vicia villosa	1	0.0417	0.2	1	

W	*Acer campestre*	1	0.333	0.58	0	***
	Elymus caninus	0.7813	0.5833	0.68	0	***
	Silene dioica	0.7801	0.7083	0.74	0	***
	Fraxinus excelsior	0.8515	0.3333	0.53	0	**
	Arctium lappa	0.9273	0.3333	0.56	0	**
	Euonymus europaeus	0.9091	0.25	0.48	0.01	**
	Festuca gigantea	1	0.2083	0.46	0.01	**
	Galium palustre	1	0.2083	0.46	0.01	*
	Veronica beccabunga	1	0.1667	0.41	0.03	*
	Anthriscus sylvestris	0.8125	0.2083	0.45	0.03	*
	Lysimachia nummularia	1	0.2083	0.41	0.03	*
	Barbarea vulgaris	0.7692	0.125	0.4	0.04	*
	Lapsana communis	0.8148	0.125	0.41	0.06	.
	Chenopodium album	1	0.125	0.35	0.09	.
	Oxalis stricta	1	0.125	0.35	0.1	.
	Hedera helix	0.9333	0.125	0.34	0.1	.
	Cardamine hirsuta	1	0.125	.035	0.1	
	Prunus spinosa	1	0.125	0.35	0.1	
	Tilia cordata	1	0.125	0.35	0.11	
	Barbarea stricta	0.8	0.1667	0.37	0.12	
	Festuca arundinacea	0.5313	0.375	0.45	0.14	
	Crataegus monogyna	0.6364	0.1667	0.33	0.17	
	Epilobium parviflorum	0.7778	0.125	0.31	0.26	
	Sinapis arvensis	1	0.0833	0.29	0.31	
	Carpinus betulus	0.9091	0.0833	0.28	0.31	
	Ranunculus ficaria	1	0.0833	0.29	0.31	
	Carex acuta	1	0.0833	0.29	0.32	
	Ballota nigra	1	0.0833	0.29	0.32	
	Barbarea verna	1	0.0833	0.29	0.32	
	Hypericum maculatum	1	0.0833	0.29	0.32	
	Plantago major	1	0.0833	0.29	0.33	
	Gnaphalium uliginosum	1	0.0833	0.29	0.34	
	Lolium multiflorum	1	0.0833	0.29	0.34	
	Agrostris capillaris	0.6191	0.1667	0.26	0.34	
	Atriplex patula	1	0.0833	0.2	0.36	
	Chelidonium majus	0.6667	0.125	0.2	0.5	
	Corylus avellana	0.8	0.0833	0.2	0.54	
	Athyrium filix-femina	1	0.417	0.2	1	
	Barbarea intermedia	1	0.417	0.2	1	
	Caltha palustris	1	0.417	0.2	1	
	Cardamine amara	1	0.417	0.2	1	
	Cardamine parviflora	1	0.417	0.2	1	
	Centaurea jacea	1	0.417	0.2	1	
	Cerastium holosteoides	1	0.417	0.2	1	
	Chenopodium polyspermum	1	0.417	0.2	1	
	Equisetum palustre	1	0.417	0.2	1	
	Erysimum cheiranthoides	1	0.417	0.2	1	
	Galium odoratum	1	0.417	0.2	1	
	Galium rotundifolium	1	0.417	0.2	1	
	Impatiens parviflora	1	0.417	0.2	1	
	Juncus bufonius	1	0.417	0.2	1	
	Mercurialis annua	1	0.417	0.2	1	
	Myosotis nemorosa	1	0.417	0.2	1	
	Nasturtium officinale	1	0.417	0.2	1	

	Polygonatum verticillatum	1	0.417	0.2	1	
	Populus tremula	1	0.417	0.2	1	
	Potentilla reptans	1	0.417	0.2	1	
	Rorippa palustris	1	0.417	0.2	1	
	Rosa spinosissima	1	0.417	0.2	1	
	Rumex obtusifolius	1	0.417	0.2	1	
	Rumex palustris	1	0.417	0.2	1	
	Salix caprea	1	0.417	0.2	1	
	Senecio vulgaris	1	0.417	0.2	1	
	Sinapis alba	1	0.417	0.2	1	
	Sisymbrium strictissimum	1	0.417	0.2	1	
	Sium latifolium	1	0.417	0.2	1	
	Trifolium dubium	1	0.417	0.2	1	
	Tripleurospermum perforatum	1	0.417	0.2	1	
	Veronica serpyllifolia	1	0.417	0.2	1	
	Viola arvensis	1	0.417	0.2	1	
U+D	*Rubus caesius*	0.8893	0.4583	0.64	0.06	.
	Elymus repens	0.8492	0.4167	0.6	0.07	.
	Lamium album	0.9692	0.2083	0.45	0.12	
	Valeriana officinalis	0.9423	0.1875	0.42	0.21	
	Stachys palustris	0.9474	0.1458	0.37	0.23	
	Scrophularia auriculata	1	0.125	0.35	0.31	
	Festuca rubra	1	0.1042	0.32	0.41	
	Hypericum perforatum	0.875	0.125	0.33	0.48	
	Tanacetum vulgaris	1	0.0833	0.29	0.54	
	Salix alba	1	0.0833	0.29	0.54	
	Geranium robertianum	1	0.0625	0.25	0.76	
	Epilobium hirsutum	1	0.0625	0.25	0.78	
	Saponaria officinalis	1	0.0417	0.2	1	
	Scrophularia umbrosa	1	0.0417	0.2	1	
U+W	*Aegopodium podagraria*	0.8785	0.625	0.74	0.01	**
	Filipendula ulmaria	0.8773	0.625	0.74	0.01	**
	Alnus glutinosa	0.9365	0.375	0.59	0.02	*
	Equisetum arvense	1	0.2292	0.48	0.04	*
	Lycopus europaeus	0.9333	0.2083	0.44	0.06	.
	Geum urbanum	0.8776	0.3125	0.52	0.07	.
	Taraxacum sect. Ruderalia	1	0.1667	0.41	0.11	
	Salix triandra	1	0.1458	0.38	0.19	
	Circaea lutetiana	1	0.1458	0.38	0.22	
	Poa pratensis	1	0.125	0.35	0.24	
	Acer pseudoplatanus	1	0.125	0.35	0.29	
	Sambucus nigra	1	0.125	0.35	0.29	
	Bromus sterilis	1	0.1042	0.32	0.36	
	Stachys sylvatica	1	0.0833	0.29	0.55	
	Vicia hirsuta	1	0.0625	0.25	0.78	
	Phleum pratense	1	0.0625	0.25	0.78	
	Dryopteris filix-mas	1	0.0417	0.2	1	
	Galeopsis pubescens	1	0.0417	0.2	1	
	Lolium perenne	1	0.0417	0.2	1	
	Quercus robur	1	0.0417	0.2	1	
	Ranunculus acris	1	0.0417	0.2	1	
	Stellaria media	1	0.0417	0.2	1	
D+W	*Symphytum officinale*	1	0.1667	0.41	0.16	
	Scutellaria galericulata	1	0.1458	0.38	0.17	

Scrophularia nodosa	1	0.1458	0.38	0.21
Juncus effusus	1	0.1042	0.32	0.33
Salix viminalis	1	0.0833	0.29	0.53
Achillea ptarmica	0.8571	0.125	0.33	0.62
Stellaria palustris	1	0.0625	0.25	0.77
Glyceria maxima	1	0.0625	0.25	0.79
Acer platanoides	1	0.0417	0.2	1
Mentha aquatica	1	0.0417	0.2	1

Appendix S4 - Overview of stand-forming species determined by indicator species analysis and their indicator values (IV). Index=7 refers to the combinations being possible across the defined groups of reaches.

Species name	Upstream	Downstream	Weir-distant	index	IV	p.value
Alliaria petiolata	1	1	1	7	0.68718427	NA
Arctium minus	1	1	1	7	0.22047928	NA
Arrhenatherum elatius	1	1	1	7	0.50689688	NA
Artemisia vulgaris	1	1	1	7	0.45643546	NA
Brachypodium sylvaticum	1	1	1	7	0.36324158	NA
Bromus inermis	1	1	1	7	0.50689688	NA
Bromus sterilis	1	1	1	7	0.26352314	NA
Calystegia sepium	1	1	1	7	0.80363756	NA
Carduus crispus	1	1	1	7	0.56519417	NA
Chaerophyllum bulbosum	1	1	1	7	0.65616732	NA
Corylus avellana	1	1	1	7	0.2763854	NA
Dactylis glomerata	1	1	1	7	0.60092521	NA
Filipendula ulmaria	1	1	1	7	0.68718427	NA
Galium aparine	1	1	1	7	0.81223286	NA
Galium mollugo	1	1	1	7	0.53359369	NA
Glechoma hederacea	1	1	1	7	0.70217915	NA
Humulus lupulus	1	1	1	7	0.49300665	NA
Hypericum perforatum	1	1	1	7	0.26352314	NA
Impatiens glandulifera	1	1	1	7	0.90905934	NA
Iris pseudacorus	1	1	1	7	0.31180478	NA
Lysimachia vulgaris	1	1	1	7	0.62360956	NA
Lythrum salicaria	1	1	1	7	0.62360956	NA
Phalaris arundinacea	1	1	1	7	0.71200031	NA
Poa palustris	1	1	1	7	0.64009548	NA
Poa trivialis	1	1	1	7	0.74535599	NA
Ranunculus repens	1	1	1	7	0.34359214	NA
Rorippa amphibia	1	1	1	7	0.23570226	NA
Rubus caesius	1	1	1	7	0.61237244	NA
Rumex crispus	1	1	1	7	0.186339	NA
Rumex sanguineus	1	1	1	7	0.25	NA
Salix fragilis	1	1	1	7	0.66143783	NA
Salix triandra	1	1	1	7	0.30046261	NA
Stellaria aquatica	1	1	1	7	0.30046261	NA
Symphytum officinale	1	1	1	7	0.34359214	NA
Urtica dioica	1	1	1	7	0.9860133	NA

Appendix S5 - Species occurrences by reaches.

Reach or reach combination	Species
Weir-distant	*Acer campestre*
	Athyrium filix-femina
	Atriplex patula
	Ballota nigra
	Barbarea intermedia
	Barbarea verna
	Caltha palustris
	Cardamine amara
	Cardamine hirsuta
	Cardamine parviflora
	Carex acutiformis
	Centaurea jacea
	Cerastium holosteoides
	Chenopodium album
	Chenopodium polyspermum
	Equisetum palustre
	Erysimum cheiranthoides
	Festuca gigantea
	Galium odoratum
	Galium palustre
	Galium rotundifolium
	Gnaphalium uliginosum
	Hypericum maculatum
	Impatiens parviflora
	Juncus bufonius
	Lolium multiflorum
	Lysimachia nummularia
	Mercurialis annua
	Myosotis nemorosa
	Nasturtium officinale
	Oxalis stricta
	Plantago major
	Polygonatum verticillatum
	Populus tremula
	Potentilla reptans
	Prunus spinosa
	Ranunculus ficaria
	Rorippa palustris
	Rosa spinosissima
	Rumex obtusifolius
	Rumex palustris
	Salix caprea
	Senecio vulgaris
	Sinapis alba
	Sinapis arvensis
	Sisymbrium strictissimum
	Sium latifolium
	Tilia cordata
	Trifolium dubium
	Tripleurospermum perforatum
	Veronica beccabunga

	Veronica serpyllifolia
	Viola arvensis
Upstream	*Achillea millefolium*
	Agrostis stolonifera
	Bromus hordeaceus
	Calystegia silvatica
	Cardamine impatiens
	Chaerophyllum temulum
	Cirsium oleraceum
	Clematis vitalba
	Cornus sanguinea
	Fagus sylvatica
	Fallopia convolvulus
	Geranium molle
	Holcus lanatus
	Myosotis sylvatica
	Origanum vulgare
	Papaver rhoeas
	Picris hieracioides
	Plantago lanceolata
	Potentilla anserina
	Prunus avium
	Ranunculus acris
	Ribes rubrum
	Rumex acetosa
	Sorbus aucuparia
	Stellaria graminea
	Trifolium pratense
	Valeriana procurrens
	Valeriana versifolia
Downstream	*Brassica nigra*
	Cruciata laevipes
	Epilobium ciliatum
	Epilobium obscurum
	Epilobium palustre
	Helianthus tuberosus
	Hypericum hirsutum
	Linaria vulgaris
	Quercus petraea
	Vicia villosa
Weir-distant + Upstream	*Acer pseudoplatanus*
	Barbarea stricta
	Barbarea vulgaris
	Bromus sterilis
	Carpinus betulus
	Chelidonium majus
	Circaea lutetiana
	Corylus avellana
	Crataegus monogyna
	Dryopteris filix-mas
	Equisetum arvense
	Euonymus europaeus
	Galeopsis pubescens
	Hedera helix

	Lapsana communis
	Lolium perenna
	Phleum pretense
	Poa pratensis
	Quercus robur
	Rumex sanguineus
	Salix triandra
	Sambucus nigra
	Stachys sylvatica
	Stellaria media
	Taraxacum sect. Ruderalia
	Vicia hirsuta
	Vicia sepium
Weir-distant + Downstream	*Acer platanoides*
	Anthriscus sylvestris
	Epilobium parviflorum
	Fraxinus excelsior
	Glyceria maxima
	Juncus effusus
	Mentha aquatica
	Salix viminalis
	Scrophularia nodosa
	Scutellaria galericulata
	Solanum dulcamara
	Stellaria palustris
	Symphytum officinale
Upstream + Downstream	*Cuscuta europaea*
	Epilobium hirsutum
	Festuca rubra
	Geranium robertianum
	Rubus vulgaris
	Salix alba
	Saponaria officinalis
	Scrophularia auriculata
	Scrophularia umbrosa
	Tanacetum vulgare
	Vicia cracca
Upstream + Downstream + Weir-distant	*Achillea ptarmica*
	Aegopodium podagraria
	Agrostis capillaris
	Alliaria petiolata
	Alnus glutinosa
	Alopecurus pratensis
	Arctium lappa
	Arctium minus
	Arrhenatherum elatius
	Artemisia vulgaris
	Brachypodium sylvaticum
	Bromus inermis
	Calystegia sepium
	Carduus crispus
	Chaerophyllum bulbosum
	Cirsium arvense
	Dactylis glomerata

	Elymus caninus
	Elymus repens
	Festuca arundinacea
	Filipendula ulmaria
	Galium aparine
	Galium mollugo
	Geum urbanum
	Glechoma hederacea
	Heracleum sphondylium
	Humulus lupulus
	Hypericum perforatum
	Impatiens glandulifera
	Iris pseudacorus
	Lamium album
	Lamium maculatum
	Lamium purpureum
	Lycopus europaeus
	Lysimachia vulgaris
	Lythrum salicaria
	Persicaria amphibia
	Phalaris arundinacea
	Phragmites australis
	Poa palustris
	Poa trivialis
	Ranunculus repens
	Rorippa amphibia
	Rubus caesius
	Rumex crispus
	Salix fragilis
	Silene dioica
	Stachys palustris
	Stellaria aquatica
	Urtica dioica
	Valeriana officinalis

Appendix S6 - Significant and not significant indicator species grouped by their habitat origin (Data retrieved from FloraWeb (KORNECK ET AL., 1998)) for upstream, downstream, weir-distant reaches and reach-independent occurences.

Reach	Habitat	Species	Percentage
Upstream	Nitrophilous tall herb communities (*Galio-Urticenea*)	*Lamium maculatum*	22
		Rumex sanguineus	
		Stellaria aquatica	
		Vicia sepium	
		Chaerophyllum temulum	
		Cardamine impatiens	
		Myosotis sylvatica	
		Picris hieracioides	
	Swamp and alluvial forests (*Alnion-glutinosae, Alno-Ulmion*)	*Phragmites australis*	16
		Rumex sanguineus	
		Ranunculus repens	
		Cirsium oleraceum	
		Clematis vitalba	
		Ribes rubrum	
	Wetland meadows (*Molinietalia caerulea*)	*Phragmites australis*	22

		Stellaria graminea *Ranunculus repens* *Valeriana procurrens* *Holcus lanatus* *Cirsium oleraceum* *Rumex acetosa* *Trifolium pratense*	
	Mesophilic meadows (*Arrhenatherion elatioris*)	*Stellaria graminea* *Ranunculus repens* *Holcus lanatus* *Bromus hordeaceus* *Vicia sepium* *Plantago lanceolata* *Rumex acetosa* *Trifolium pratense*	22
	Flooded meadows, grasslands on trampled ground (*Agrostietea stoloniferae, Plantaginetea majoris*)	*Ranunculus repens* *Potentilla anserina*	5
	Bur-marigold and orache bank communities (*Bidentetea*)	-	0
	Arable land, annual ruderal communities (*Chenopodietea*)	*Ranunculus repens* *Bromus hordeaceus* *Fallopia convolvulus* *Geranium molle* *Papaver rhoeas*	13
Downstream	Nitrophilous tall herb communities (*Galio-Urticenea*)	*Cuscuta europaea* *Brassica nigra* *Linaria vulgaris* *Solanum dulcamara* *Cruciata laevipes* *Hypericum hirsutum*	67
	Swamp and alluvial forests (*Alnion-glutinosae, Alno-Ulmion*)	-	0
	Wetland meadows (*Molinietalia caerulea*)	*Vicia cracca*	11
	Mesophilic meadows (*Arrhenatherion elatioris*)	*Vicia cracca*	11
	Flooded meadows, grasslands on trampled ground (*Agrostietea stoloniferae, Plantaginetea majoris*)	*Rorippa amphibia*	11
	Bur-marigold and orache bank communities (*Bidentetea*)	-	0
	Arable land, annual ruderal communities (*Chenopodietea*)	-	0
Weir-distant	Nitrophilous tall herb communities (*Galio-Urticenea*)	*Elymus caninus* *Silene dioica* *Arctium lappa* *Festuca gigantea* *Anthriscus sylvestris* *Barbarea vulgaris* *Lapsana communis* *Barbarea stricta* *Ficaria verna* *Ballota nigra* *Chelidonium majus* *Erysimum cheiranthoides*	21

		Rumex obtusifolius *Sisymbrium strictissimum*	
	Swamp and alluvial forests (*Alnion-glutinosae, Alno-Ulmion*)	*Acer campestre* *Elymus caninus* *Silene dioica* *Fraxinus excelsior* *Euonymus europaeus* *Festuca gigantea* *Lysimachia nummularia* *Hedera helix* *Ficaria verna* *Carex acutiformis* *Corylus avellana* *Athyrium filix-femina* *Caltha palustris* *Cardamine amara* *Polygonatum verticillatum* *Myosotis nemorosa*	24
	Wetland meadows (*Molinietalia caerulea*)	*Ficaria verna* *Hypericum maculatum* *Myosotis nemorosa*	5
	Mesophilic meadows (*Arrhenatherion elatioris*)	*Silene dioica* *Anthriscus sylvestris* *Lysimachia nummularia* *Ficaria verna* *Agrostis capillaris* *Centaurea jacea* *Cerastium holosteoides* *Trifolium dubium* *Veronica serpyllifolia*	13
	Flooded meadows, grasslands on trampled ground (*Agrostietea stoloniferae, Plantaginetea majoris*)	*Lysimachia nummularia* *Barbarea vulgaris* *Barbarea stricta* *Festuca arundinacea* *Plantago major* *Cardamine parviflora* *Potentilla reptans* *Rumex obtusifolius* *Veronica serpyllifolia*	13
	Bur-marigold and orache bank communities (*Bidentetea*)	*Chenopodium polyspermum* *Erysimum cheiranthoides* *Rorippa palustris* *Rumex palustris*	6
	Arable land, annual ruderal communities (*Chenopodietea*)	*Chenopodium album* *Cardamine hirsuta* *Sinapis arvensis* *Gnaphalium uliginosum* *Atriplex patula* *Chenopodium polyspermum* *Erysimum cheiranthoides* *Juncus bufonius* *Mercurialis annua* *Senecio vulgaris* *Tripleurospermum perforatum*	18

		Viola arvensis	
Reach-independent	Nitrophilous tall herb communities (*Galio-Urticenea*)	*Alliaria petiolata* *Arctium minus* *Arrhenatherum elatius* *Artemisia vulgaris* *Bromus inermis* *Calystegia sepium* *Carduus crispus* *Chaerophyllum bulbosum* *Dactylis glomerata* *Galium aparine* *Galium mollugo* *Glechoma hederacea* *Humulus lupulus* *Hypericum perforatum* *Poa palustris* *Poa trivialis* *Rubus caesius* *Rumex sanguineus* *Stellaria aquatica* *Symphytum officinale* *Urtica dioica*	37
	Swamp and alluvial forests (*Alnion-glutinosae, Alno-Ulmion*)	*Brachypodium sylvaticum* *Corylus avellana* *Filipendula ulmaria* *Glechoma hederacea* *Humulus lupulus* *Iris pseudacorus* *Lysimachia vulgaris* *Ranunculus repens* *Rubus caesius* *Rumex sanguineus* *Salix fragilis* *Salix triandra* *Symphytum officinale* *Urtica dioica*	25
	Wetland meadows (*Molinietalia caerulea*)	*Dactylis glomerata* *Filipendula ulmaria* *Galium mollugo* *Lysimachia vulgaris* *Lythrum salicaria* *Poa palustris* *Poa trivialis* *Ranunculus repens* *Symphytum officinale*	16
	Mesophilic meadows (*Arrhenatherion elatioris*)	*Arrhenatherum elatius* *Dactylis glomerata* *Glechoma hederacea* *Poa trivialis* *Ranunculus repens*	9
	Flooded meadows, grasslands on trampled ground (*Agrostietea stoloniferae, Plantaginetea majoris*)	*Poa trivialis* *Ranunculus repens* *Rorippa amphibia* *Rumex crispus*	13

		Symphytum officinale	
	Bur-marigold and orache bank communities (*Bidentetea*)	-	6
	Arable land, annual ruderal communities (*Chenopodietea*)	*Galium aparine* *Ranunculus repens*	4

Abstract

Rivers have always been used as transport medium for goods, which still applies to large rivers like the Main, the Danube or the Rhine. Thus, regulation measures were necessary to meet the criteria for navigation. River and floodplain ecosystems, formerly defined by their dynamic character, are therefore confronted with enormous changes in ecosystem functioning, being displayed by reduced functionality of ecosystem services and i. a. distinct changes in plant species composition. The European Water Policy thus adopted the Water Framework Directive, aiming at achieving the good ecological status for all European rivers by 2027, whereby the goal of the good ecological potential is intended for highly regulated water bodies like German Federal Waterways. In which way this can be realized for riverbanks along Federal Waterways and how the success of riverbank revitalization measures can be evaluated, is the subject of this work.

To this end, vegetation was sampled along riverbanks of the Main, Danube, Lahn and Fulda during the growing seasons 2016, 2017 and 2018. All rivers are intensively affected by impoundments and riverbank embankments consisting of ripraps. Data analysis was carried out by means of multivariate and univariate statistical approaches and revealed homogeneity in riverbank species composition, although these habitats are naturally characterized by a high level of heterogeneity. Species composition mainly consisted of competitive species, which originally occur in habitats in more distance to the river, as these species reveal no adaptations to recurring flooding events. Typical riverbank species were less frequent and grew in dominance along flat riverbank sites (6%) with higher intensity in water level fluctuations. Thus, the lowering of bank steepness is considered to be effective for promoting species with improved adaptations to changing water levels. The second field study conducted for this dissertation revealed that lowering of bank steepness will be most successful in areas, where averagely higher water level fluctuations are existent. This especially applies to downstream reaches of weirs, which are mainly distributed along secondary Federal Waterways and which are not influenced by the next weir downstream, as water level fluctuations will decline gradually with growing proximity to the next weir. By contrast to secondary Federal Waterways, the areas directly influenced by impoundments (one kilometer upstream and downstream of impoundments) reveal a too high regulation intensity, wherefore these areas are recommended to remain unconsidered for riverbank restoration measures.

Furthermore, it is also possible to actively manage the restored species composition by bank structure. Concave flat banks without ripraps but with gravel addition in the transition zone between water and land revealed the most typical species composition for riverbanks. By contrast, species composition of banks that were front-fixed by ripraps in the waterway´s channel was also enriched by species from low-flow to stagnant habitats. The results of the first field study for this work revealed that the removal of ripraps can promote a higher lateral connectivity between river

and floodplain and a higher level of heterogeneity in riverbank habitats. Thus, unfortified and front-fixed banks can essentially contribute to biotope-cross linking along Federal Waterways. Due to reasons of traffic safety, the removal of ripraps is largely not feasible along primary Federal Waterways, wherefore riverbank restoration measures are limited to local measures. As secondary waterways are mainly used for leisure purposes, riverbank erosion events that are induced by shipping traffic are not expected. Further, water flow velocity is significantly reduced along upstream areas within a distance of one kilometer to the next weir. Compared to primary Federal Waterways, there thus exist more space for riprap removals along secondary Federal Waterways.

As the character of plant species diversity measures is rather descriptive and these measures are not applicable to display species´ adaptation to recurring disturbance events, this approach is not recommendable for the evaluation of riverbank restoration measures. Therefore, this evaluation was carried out by means of species traits of the potential natural vegetation of riverbanks, consisting mainly of low competitive and annual species. Restoration measures were considered to be successful when species composition was characterized by more species with the mentioned traits compared to the basis of comparison (banks protected by ripraps, banks along upstream reaches with reduced hydrodynamic compared to downstream reaches). The analysis of species traits further considered species´ habitat origin and led to the conclusion that *Bidentetea* species were too rare for a sound evaluation of riverbank restoration measures. As species from flooded meadows displayed the intensity of water level fluctuations much better than *Bidentetea* species and also originate from riverbank transition zones, they attach great importance in this context.

Zusammenfassung

Die Flüsse unserer Landschaft wurden seit jeher als Transportmedium für Güter genutzt. Dies ist insbesondere für die großen Flüsse wie Main, Donau oder Rhein immer noch von Relevanz, weshalb sie im Laufe der Zeit zu Bundeswasserstraßen ausgebaut wurden, die den Anforderungen des Schiffsverkehrs gerecht werden müssen. Das ehemals von Dynamik geprägte Ökosystem Fluss-Aue sieht sich deshalb mit tiefgreifenden Veränderungen konfrontiert, die mit einer eingeschränkten Funktionalität der Ökosystemleistungen und unter anderem wesentlichen Veränderungen im floristischen Artengefüge einhergehen. Die europäische Wasserpolitik möchte deshalb im Rahmen der Wasserrahmenrichtlinie bis zum Jahr 2027 mithilfe geeigneter Maßnahmen den guten ökologischen Zustand aller europäischen Fließgewässer erreichen, wobei für die stark genutzten und ausgebauten Bundeswasserstraßen die Erreichung eines guten ökologischen Potentials angestrebt wird. Auf welche Weise dies für die Uferzonen der Bundeswasserstraßen erreicht werden kann und wie der Erfolg von Uferrevitalisierungsmaßnahmen an stark regulierten Fließgewässern bemessen werden kann, ist Gegenstand dieser Dissertation.

Zu diesem Zweck wurden in den Vegetationsperioden 2016, 2017 und 2018 Vegetationsaufnahmen in den Uferzonen von Main, Donau, Lahn und Fulda erhoben, die durch Querbauwerke und Uferbefestigungen aus Steinen im Hinblick auf die Hydrodynamik stark reguliert sind. Die Daten wurden mithilfe multivariater und univariater statistischer Methoden analysiert und zeichnen ein homogenes Bild der ehemals von Heterogenität geprägten Artenzusammensetzung in den Uferbereichen. Hohe Anteile an konkurrenzstarken Arten charakterisieren die heutigen Uferzonen der Fließgewässer, die natürlicherweise aufgrund der häufig wiederkehrenden Überflutungen in den Uferhabitaten in flussfernen Habitaten anzutreffen sind. Typische Arten der Uferbereiche kamen in geringen Anteilen vor und waren vor allem in Bereichen mit geringerer Uferneigung (6%) dominanter, wo aufgrund der strukturellen Standortgegebenheiten eine höhere Intensität von Wasserstandsschwankungen zu erwarten ist. Eine effiziente Maßnahme zur Förderung von stärker spezialisierten Arten ist aus diesem Grund die Abflachung der Ufer, die vorrangig in den Bereichen vorzunehmen ist, in denen durchschnittlich stärkere Wasserstandsschwankungen zu erwarten sind. Dies gilt vorranging für die wehrunterhalb gelegenen Bereiche an den Nebenwasserstraßen, wobei darauf geachtet werden sollte, dass der Einflussbereich der weiter unterhalb befindlichen Stauanlage in diesem Zusammenhang unberücksichtigt bleibt, da die Wasserstandsschwankungen mit zunehmender Nähe zum nächsten Wehr erneut graduell sinken. Die direkt durch die Staustufen beeinflussten Bereiche (ein Kilometer vor und nach jeder Staustufe) der Wasserstraßen im Hauptnetz hingegen sind von zu starker Regulierung überprägt, weshalb in diesem Bereich von Uferrevitalisierungsmaßnahmen eher abzusehen ist.

Über die Uferstrukturierung besteht zudem die Möglichkeit, die Artenzusammensetzung in den Uferbereichen zu lenken. Eingebuchtete abgeflachte Ufer ohne Uferbefestigung aus Blocksteinen, jedoch mit Kieszugabe in den Übergangszonen zwischen Wasser und Land, zeigten in diesem Zusammenhang die standorttypischste Artenzusammensetzung. Dagegen wurden in Uferbereichen, die durch vorgelagerte Steinschüttungen im Flussbett vor Wellenschlag geschützt werden, auch Arten aus strömungsarmen Habitaten beobachtet. Im Rahmen der ersten Feldstudie für diese Dissertation zeigte sich, dass ein sparsamer Umgang mit Blocksteinen in den Uferzonen der Bundeswasserstraßen zu einer verstärkten lateralen Konnektivität zwischen Fluss und Aue beitragen kann und die Standortheterogenität in den Uferzonen positiv beeinflusst. Damit leisten unbefestigte Ufer und Ufer mit vorgelagerten Steinschüttungen einen wesentlichen Beitrag für die Biotopvernetzung an Bundeswasserstraßen. Die Entsteinung der Ufer ist an den Hauptwasserstraßen aus Verkehrssicherungsgründen weitestgehend nicht praktikabel, weshalb Uferrevitalisierungsmaßnahmen nur lokal realisiert werden können. An den gestauten Nebenwasserstraßen hingegen besteht vor allem in den direkt staubeeinflussten Bereichen die Möglichkeit der großflächigen Uferentsteinung, da die Fließgeschwindigkeit in diesen Bereich deutlich reduziert ist und Ufererosion durch Wellenschlag aufgrund der Beschränkung auf die Nutzung zu Freizeitzwecken nicht zu erwarten ist.

Die Bemessung des Erfolgs von Uferrevitalisierungsmaßnahmen anhand von Parametern zur Quantifizierung der Artendiversität ist nicht zu empfehlen, da diese Maße keine Aussage über die Spezialisierung der Arten hinsichtlich wiederkehrender Störungsereignisse treffen können. Aus diesem Grund erfolgte die Bemessung des Erfolgs von Uferrevitalisierungsmaßnahmen im Rahmen dieser Arbeit anhand der Arteigenschaften der potentiellen natürlichen Vegetation von Uferzonen. Diese besteht zu einem wesentlichen Anteil aus konkurrenzschwachen und kurzlebigen Arten, weshalb Uferrevitalisierungsmaßnahmen als erfolgreich bewertet wurden, wenn die Artenzusammensetzung durch einen höheren Anteil dieser Arten im Vergleich zur Vergleichsgrundlage (durch Steinschüttungen befestigte Ufer, Ufer mit reduzierter Hydrodynamik) charakterisiert war. Die Analyse der Arteigenschaften schloss darüber hinaus auch die Habitatherkunft der Arten ein. Es zeigte sich, dass die Arten der Zweizahn-Pionierfluren aufgrund ihrer Seltenheit ungeeignet für die Beurteilung des Erfolgs von Uferrevitalisierungsmaßnahmen an stark regulierten Fließgewässern sind. Da die Arten der Flutrasen die Intensität der Wasserstandsschwankungen regulierter Uferbereiche besser wiederspiegeln konnten und diese wie die Arten der Zweizahn-Pionierfluren in den Wechselwasserzonen von Ufern beheimatet sind, wird diesen Arten bei der Erfolgsbewertung von Uferrevitalisierungsmaßnahmen an regulierten Fließgewässern eine hohe Bedeutung beigemessen.

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Declaration

I declare that I have completed this dissertation single-handedly without the unauthorized help of a second party and only with the assistance acknowledged therein. I have appropriately acknowledged and cited all text passages that are derived verbatim from or are based on the content of published work of others, and all information relating to verbal communications. I consent to the use of an anti-plagiarism software to check my thesis. I have abided by the principles of good scientific conduct laid down in the charter of the Justus Liebig University Giessen „Satzung der Justus-Liebig-Universität Gießen zur Sicherung guter wissenschaftlicher Praxis“ in carrying out the investigations described in the dissertation.

Gießen, 29. November 2019

Julia-Teresa Wollny