

Anthropogenic influence on the distribution patterns of plant species and habitat diversity along German Federal Waterways



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Chapter 1

Anthropogenic influence on the distribution patterns of biodiversity along German Federal Waterways – A synthesis

In this chapter, the theoretical background and framework for this thesis are introduced. It highlights the main objectives of this work and provides an overview of the two manuscripts the thesis is based on. The main results and conclusions are presented and recommendations for an ecological management of Waterways are developed.



1.1 Introduction

1.1.1 Background

Riparian systems

Natural rivers and their floodplains are among the most species-rich, complex and dynamic habitats in the world (Naiman *et al.*, 1993). Riparian areas form ecotones between aquatic and terrestrial environments (Brown *et al.*, 1979), since they comprise the river channel and the (terrestrial) area that is influenced by flooding (Ellenberg, 2009, p.243). They are characterized by strong ecological gradients and dynamics: The flooding and sedimentation regime, the lateral shift of the river channel which causes small-scale soil and topographic heterogeneity, climatic variation, and disturbance from adjacent areas lead to a dynamic mosaic of environmental conditions and habitats; these factors result in high levels of biodiversity, as reviewed by Naiman *et al.* (1993).

The natural floodplain vegetation is adapted to dynamic conditions. Most species can tolerate periods of flooding as well as periods of drought (Ellenberg, 2009, p.244). The amphibious river banks are dominated by quick growing annual species. In the lower reaches, these areas are vegetated by reed strips (Ellenberg, 2009, p.248). With increasing distance to the river, the natural floodplain vegetation comprises willow scrubs and alluvial forests, which are mainly composed of *Salix* or *Populus* species where flooding occurs frequently, or *Fraxinus*, *Ulmus* or *Quercus* species where flooding is less frequent (Ellenberg, 2009, p.246, 249). *Salix alba* has a flooding tolerance of up to 180 days during the vegetation period, while *Quercus robur* can tolerate up to 62 days and *Fraxinus excelsior* up to 27 days of flooding during the vegetation period (April – September) without visible damage (long term mean, Ellenberg & Leuschner, 2010, p. 463).

These vegetation stages are changing in space and time. Zonation and succession processes are regulated by the dynamics of the river that induce erosion and sedimentation and lead to small-scale vegetation patterns (Ellenberg, 2009, p.252) and, hence, a high species diversity, as described by Naiman and Decamps (1997) in their extensive review on the character of riparian zones.

Riparian systems provide several ecosystem functions, e.g. sediment transport and deposition, flood retention, groundwater re- and discharge, nutrient filtration and storage as well as carbon sequestration (Maltby *et al.*, 2009; Naiman and Decamps, 1997; Scholz *et al.*, 2012). They serve as ecological corridors for species dispersal and they provide

habitat space, which results in exceptionally high levels of biodiversity (Naiman and Decamps, 1997). Vice versa, biodiversity is an important driver of ecosystem functionality, as found e.g. by Naeem *et al.* (1994) in an experimental study on the influence of reduced diversity on ecosystem processes on several trophic levels. Later this was also acknowledged in the Millennium Ecosystem Assessment (MEA, 2005). Therefore, the protection of floodplain biodiversity, especially from anthropogenic endangerment, is in the focus of politics and research and the central aim of this dissertation.

Anthropogenic influence on floodplains

Humans have always utilized the functions of riparian ecosystems for their purposes, e.g. the use of the river for transportation, i.e. shipping traffic, agricultural use of the fertile soils in the floodplain areas, collection of drinking and irrigation water, or hydropower generation (Malanson, 1993, p.16 *ff.*; Scholz *et al.*, 2012). They have altered riparian systems to meet their requirements (Malanson, 1993, p.18 *ff.*). Clear-cutting of riparian forests started in the neolithic age, and since the industrial revolution in the early nineteenth century, alterations of the river channel, flood protection measures, hydropower production and flow regulation have fundamentally changed the rivers and floodplains in Europe and North America, as reported by Naiman and Decamps (1997).

By the end of the last century, 77 % of the rivers in Europe, the Commonwealth of Independent States (CIS), and North America were seriously modified (Cowx & Welcomme, 1998). In Germany, the first exhaustive floodplain inventory showed that modification and flood control measures led to a loss of two thirds of the original (historical) floodplain area (Brunotte *et al.*, 2009). The remaining floodplains are of low ecological value: only ten percent of them could be regarded to be in an ecologically functional state (Brunotte *et al.*, 2009).

Since the biodiversity of riparian systems is dependent on the runoff regime and dynamic changes of stream morphology, alterations of these processes cause the most substantial changes in riparian vegetation (Naiman and Decamps, 1997). Barrages (e.g. for hydropower generation) alter flow and sedimentation, they influence water temperature and quality, and the channel shape is changed due to reduced meandering (an overview is given in the textbooks by Allan and Castillo, 2007, chapter 13; or Malanson, 1993, p.19 *ff.*). These civil engineering works reduce the connectivity between river water and floodplain since the runoff is regulated and flooding is inhibited. Dams inhibit flooding,

the main driver of floodplain biodiversity, thus they have profound effects on those species depending on dynamic conditions (Malanson, 1993, p.20 ff., p.114). The direction of these effects is however differing between different studies. Dynesius *et al.* (2004) did not find differences in species richness between regulated and unregulated rivers, whereas Chipps *et al.* (2006) or Poff and Zimmerman (2010) report a decline in species diversity, and Deiller *et al.* (2001) show that species richness increased in a riparian forest with reduced flooding influence.

Channelization of streams is defined as the straightening of the river channel to increase drainage (Malanson, 1993, p.117) and thus to gain more land for agriculture, and to improve the conditions for shipping traffic (Allan and Castillo, 2007, p.327). The effects are manifold: the flow velocity increases, the stream incises more deeply, which decreases the connectivity of surface water between the stream and the floodplain terraces. The landscape is drained, consequently the hydrological conditions in the floodplain change fundamentally. Moreover, the changes in flow velocity and morphology require bank stabilization measures (rip rap or walls) which further isolate the floodplain from the stream and destroy the original bank vegetation, as found by Shields (1991) in a study on the rip rap along the Sacramento River. When comparing the floodplain vegetation of natural and channelized rivers, many studies report a shift in species composition towards more terrestrial species along the channelized rivers due to the hydrological differences, as reviewed e.g. by Poff and Zimmerman (2010).

The construction of artificial canals for navigation or irrigation purposes connects otherwise distinct aquatic systems (Allan and Castillo, 2007, p.328) and might enhance the spread of invasive species, such as the quagga mussel (*Dreissena rostriformis bugensis*) which was likely introduced to Western Europe via the Main-Danube Canal (Heiler *et al.*, 2013). On the other hand, canals might serve as refuge habitats for endangered riparian species (see the review by Chester and Robson, 2013), but in general, the ecological functions of man-made canals – at least in relation to floristic diversity - have rarely been studied (but see e.g. Goulder, 2008).

One of the most important drivers of biodiversity in a landscape is intensive land use (Waldhardt, 2003). Next to the flooding regime, Méndez-Toribio *et al.* (2014) also identified intensive land use as an important factor for the floristic diversity in floodplain landscapes. Agricultural production is a source for sediment, nutrient and pesticide runoff which leads to elevated concentrations in the river water, as reported by Bondar *et al.* (2007) in a guidance document for the integration of nutrient retention in wetland

management in Austria. It also causes negative edge effects on floodplain habitats (Méndez-Toribio *et al.*, 2014). Moreover, intensive land use results in a loss of habitat and retention area for flood protection (Brunotte *et al.*, 2009; Scholz *et al.*, 2012). Nowadays, many rivers are subject to a multitude of anthropogenic alterations and influences, which lead to a transition of the riparian vegetation communities away from a natural state (as found e.g. by Baart *et al.*, 2013 in historical analyses of the Danube floodplain) towards homogenized, simplified habitats (Allan and Castillo, 2007, p.317). However, it is difficult to predict how these alterations affect riparian landscapes when acting in concert and whether the patterns remain similar across regions (but see the study comparing several rivers in France, Spain and the US by Tabacchi *et al.*, 1996). Since riparian systems are unique and react individually, it is difficult to draw general conclusions (as argued by Bendix and Hupp, 2000) and consequently, most research on the anthropogenic influence on rivers and floodplains is conducted as case studies, e.g. concerning the riparian vegetation along the Morava River in Slovakia or the macrophyte communities of the Rio Paraná in Brazil (Banasova *et al.*, 2004; Martins *et al.*, 2013). The aim of this thesis was to fill this knowledge gap by analyzing a canal and several rivers with differing degrees of construction and management intensities and thus to determine whether the effects of human influence remain visible and comparable on a broad scale.

Biodiversity in a floodplain context

The negative effects of human actions on floodplains and the dimension of these alterations have been acknowledged by authorities and legislations. Thus floodplains and their value as hot spots of biodiversity are of special importance in the Ramsar Convention on Wetlands (United Nations, 1971), the European Habitats Directive (The Council of the European Communities, 1992), the Convention on Biodiversity (CBD, United Nations, 1992), and the Millennium Ecosystem Assessment (MEA, 2005). However, the definitions and indicators for ‘biodiversity’ are manifold and it is not always clear which terminology is used, not only in a floodplain context. In this chapter, the definitions and the measures used in this thesis will be briefly summarized.

The probably most comprehensive definition of biodiversity is given by Noss (1990): He characterizes biodiversity by relating the three attributes of ecosystems as described by Franklin (1981), namely ‘composition’, ‘structure’ and ‘function’, to the (hierarchical) organizational levels of life, i.e. genes, populations, communities and landscapes. In his

approach, composition includes the identity and diversity of genotypes, species or other entities. Structure is described as patterns of systems, e.g. the organization of entities within communities or of habitats within landscapes. Function is related to ecological processes, such as communication, interaction, but also nutrient cycles and other processes that include abiotic factors (Noss, 1990).

His approach echoes in the definition provided in the Convention on Biodiversity (United Nations, 1992): “Biological diversity means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems” (United Nations, 1992). This includes the genetic diversity, species diversity, and diversity of habitats. In this work, the focus lies on the diversity of plant species and habitats, i.e. composition and structure on the species and ecosystem level.

To measure biodiversity, Noss (1990) states that no single indicator will meet the requirements of sufficient sensitivity, applicability, independence, cost-effectiveness or relevance, therefore he suggests to apply a set of complementary indicators. The terms introduced by Whittaker (1960) are frequently used when comparing the diversity of species across communities or ecological gradients, as it is the case in floodplains: *Alpha diversity* describes the diversity of species within a habitat or a site, *beta diversity* describes how two or more sites differ in their composition, *gamma diversity* is the sum of alpha and beta diversity and, thus, the diversity of the landscape (Whittaker, 1960). For alpha diversity, Peet (1974) suggests that next to richness (the number of species), also heterogeneity (the relative abundance of species) and equitability (the dominance of species) should be considered. The frequently used Shannon index (Shannon and Weaver, 1963) includes abundance (or relative coverage in case of plant species), the Simpson index (Simpson, 1949) or Hill’s evenness (Hill, 1973) include dominance. Despite being controversially discussed (e.g. Buckland *et al.*, 2005), these indices are still among the most frequently employed measures of biodiversity (2,904 and 860 records for ‘Shannon index’ and ‘Simpson index’, respectively, in the Web of Science between 2010 and 2014). Beta diversity describes the compositional differences between sites (Whittaker, 1960). The analysis of species composition gives insight into species traits and characteristics. In a floodplain context, this is especially relevant when studying species adaptation to the special ecological conditions. Phytodiversity of floodplains is driven by river dynamics (Naiman *et al.*, 1993) and plant species are often specialized. In this thesis, plant species

composition and the functional diversity of plant species were indicative for the degree of human impact on the studied habitats.

Function is one key aspect of biodiversity on all organizational levels (Noss, 1990). Since the interest in ecosystem processes and ecosystem functions has been increasing since the 1990s, the functional aspect of biodiversity has received increasing attention in biodiversity research, as reviewed by Diaz and Cabido (2001). For the measurement of this functional aspect (hereafter termed '*functional diversity*'), several definitions and indicators have been developed.

One of the first definitions was given by Steele (1991) in his work on the functional diversity of marine ecosystems: functional diversity is "the variety of different responses to environmental change". Since functional diversity plays a role on every organizational level and in some cases connects several levels, Steele (1991) already suggests it as a separate component standing next to genetic, species and ecosystem diversity (as nowadays widely acknowledged in contrast to the concept of Noss, see e.g. Diaz and Cabido, 2001).

In the 1990s, a widely accepted method to measure functional diversity was to measure the diversity of functional groups in an ecosystem (Martinez, 1996, p.123), also referred to as 'functional group diversity' (Tilman, 2001). In this approach, species that are functionally similar are assigned to functional groups (e.g. herbs, grasses, legumes) and the diversity and composition of these groups is analyzed. Tilman *et al.* (1997) could thus relate functional composition and functional diversity to ecosystem processes. In their study, the diversity and composition of functional groups based on physiological and morphological traits (e.g. the ability to fix nitrogen, C3 vs. C4 photosynthetic pathways) influenced the productivity and the nitrogen cycle of the studied grassland ecosystem more effectively than plant species diversity and species composition (Tilman *et al.*, 1997). In 2001, Tilman provided a widely acknowledged definition of functional diversity as "the range and value of those species and organismal traits that influence ecosystem functioning" (Tilman, 2001, p.109). Mason *et al.* (2005) argue that this definition requires precisely defined methods to measure functional diversity. They see the functional group approach (which was not directly related to that definition of Tilman, but still widely applied, Mason *et al.*, 2005) as problematic since the functional groups need to be defined a priori, which may cause a bias in data analysis (Mason *et al.*, 2005). Relying on Rosenfeld (2002), who relates functional diversity to niche theory, Mason *et al.* (2005) define functional diversity as "the distribution of the species and abundance of a community in niche space" (p.114).

For a comprehensive description of the concept, they suggest three aspects of functional diversity, namely functional richness, i.e. the functional niche space occupied by the species present, functional evenness, i.e. the evenness of the distribution of abundances within this niche space, and functional divergence, i.e. the divergence of the (abundance-weighted) distribution within the functional trait space. Many indices have been developed based on this definition that are nowadays widely applied (e.g. by Villéger *et al.*, 2008, see also the review by Mouchet *et al.*, 2010). In the present work, we analyze the functional diversity of plant species by applying indices that capture all aspects, functional richness, functional evenness and functional divergence (compare chapter 3).

Landscape diversity refers to composition and structure of habitat patches on the landscape level (after Noss, 1990). It influences the beta and gamma diversity of species on a landscape scale (Whittaker, 1960), and it is included as an important factor of diversity in the CBD (United Nations, 1992). Diverse landscape features provide habitat space for a higher diversity of species, and edge effects along habitat borders further influence species distribution (Kumar *et al.*, 2006). In floodplains, plant species diversity is based on the dynamic shifting of habitats in space and time and on the diversity of habitats (Naiman *et al.*, 1993), thus landscape diversity is one of the main drivers of biodiversity in those landscapes. Therefore, landscape diversity and habitat diversity played an important role in this thesis, and they were used in to interpret the results of the plant species inventories.

Buckland *et al.* (2005) conclude that it requires a set of indices to capture as many aspects of biodiversity as possible. In accordance with this conclusion, this dissertation is based on the analysis of the following aspects:

The richness and diversity of plant species, i.e. the composition of riparian vegetation on the community level, was studied along German Federal Waterways in a comparative study along several rivers (chapter 2) and in a case study comparing a river and a canal (chapter 3). In both studies, the most common species and indicator species were further analyzed with regard to functional traits that are meaningful for a floodplain context (wetness and flooding tolerance, life strategy). In chapter 3, functional diversity of plant species was considered, i.e. indicators for the functional aspect of diversity on the community level were analyzed additionally. Finally, the diversity of habitats within the respective landscapes (composition and structure on the ecosystem/landscape level) was studied in both manuscripts, first as a possible influencing factor for the diversity of plant species, and second as an indicator for the biodiversity of the considered ecosystems by

itself. Thus the aim was to capture as many elements of biodiversity as possible to provide a comprehensive overview of the biodiversity along German Federal Waterways.

1.1.2 Objective and study questions

The main objectives of this work were to inventory the plant species diversity in the floodplains and adjacent areas¹ of the German Federal Waterways, to identify the relevant correlations between plant species distribution, floristic diversity and natural as well as anthropogenic determinants, and to draw implications for a more sustainable waterway management.

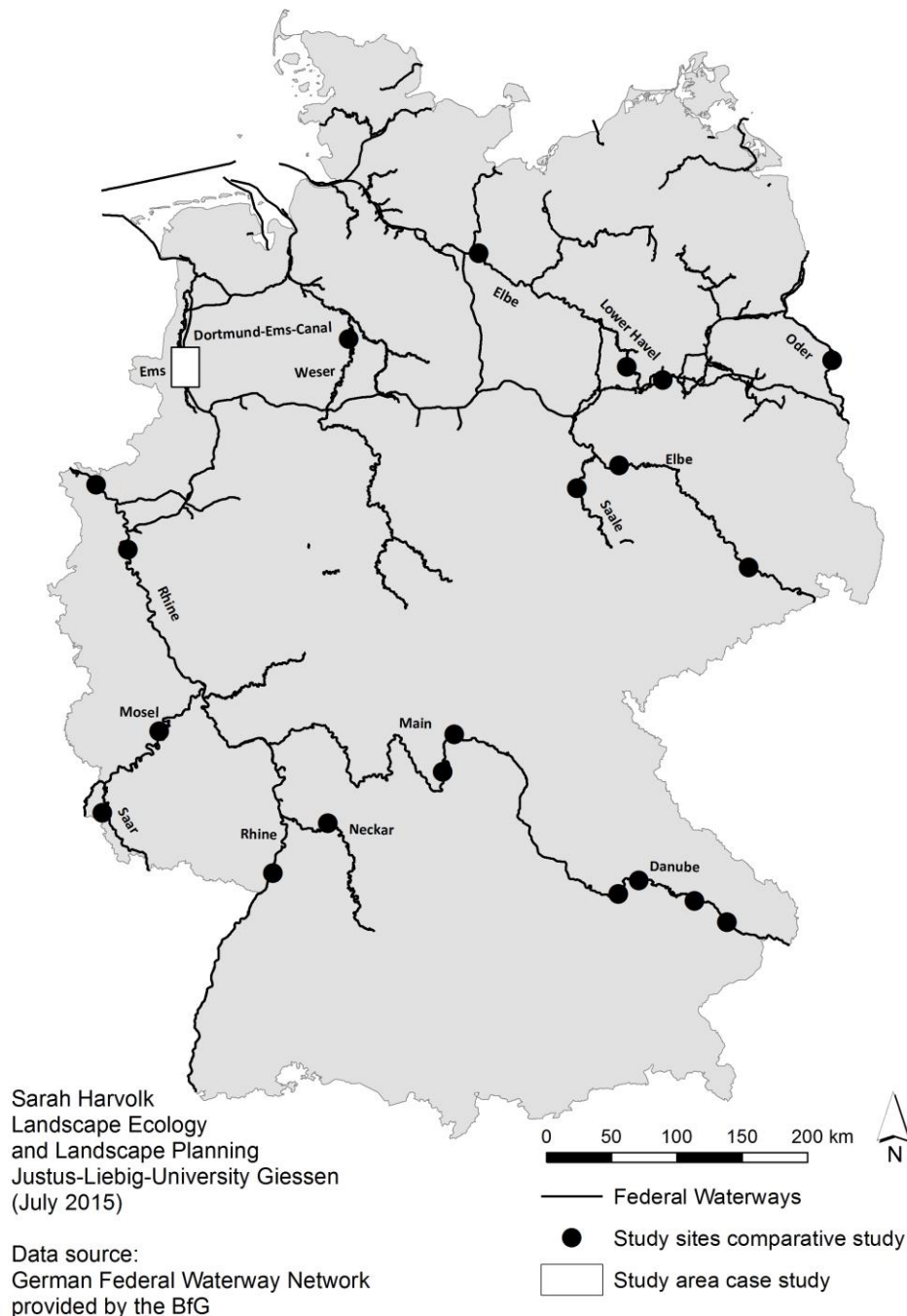
In this context, this thesis aims to answer the following questions:

- 1) Which plant species occur in the floodplain habitats along German Federal Waterways, i.e. rivers and canals?
- 2) Do these habitats provide space for typical and/or endangered floodplain plant species?
- 3) In which way are plant species diversity and its functional diversity related to each other and how do they differ between a river and a canal?
- 4) Which factors are related to plant species composition and species diversity indices on different scales in the study areas, what is the role of habitat diversity?
- 5) What is the relative impact of river management on species composition and diversity indices in comparison to natural regional differences?
- 6) Which conclusions can be drawn from this work for the management of phytodiversity and habitat diversity along waterways?

¹ This term is used for the adjacent areas of canals since floodplains exist only for rivers of natural origin.

1.2 Study Region

German Federal Waterways are navigable surface waters under state administration. They make up 29.8 % of the German surface waters (total length: 6900 km, total surface: 2320 km²) (Wolter, 2001). 77 % of the Federal Waterways are rivers and streams, 23 % are artificial canals (Wolter, 2001). Since the largest rivers in Germany belong to the Federal Waterways (Wolter, 2001), they are of substantial importance for the conservation of riparian biodiversity.



*Figure 1-1: Map of the German Federal Waterways.
Circles indicate the study sites of the comparative study in chapter 2.
The square indicates the study area of the case study in chapter 3.*

The German Federal Waterways are managed by one administration, consequently management follows similar regulations. Thus, they serve as a good example to study effects of river regulation, construction and maintenance.

Germany is located in the center of Europe and covers a wide geographic range from the Alps to the coastal areas of the North Sea and the Baltic Sea and from oceanic to continental climate. The water bodies studied in this dissertation cover the riparian landscape zones in uplands and lowlands (applying a modified version of the zonation defined by Koenzen 2005). Since none of the river stretches in Alpine regions are designated as Federal Waterways, the Alps were excluded in this work. Estuaries were excluded as well since they are in the focus of many other research projects (e.g. Engels & Jensen, 2009) due to their complex hydrological and ecological conditions.

The study sites for the comparative study (chapter 2, fig. 1-1) were selected applying a stratified random sampling regime, so that they are equally distributed between uplands and lowlands, comprising river stretches with strong and weak inclination and with and without regulation by barrages. Thus they present a representative selection of German Federal Waterways.

The case study was conducted along a stretch of the Dortmund-Ems-Canal between the towns Lingen and Meppen in North-Western Germany (chapter 3, fig.1-1). In this area, the canal flows in parallel to the non-shippable part of the river Ems, both water bodies are hydrologically connected. This unique situation allowed for a direct comparison between a canal and a river.

1.3 Chapter Outline

This thesis is based on two manuscripts; both have been accepted for publication by international peer-reviewed scientific journals, one of the manuscripts is already published.

Chapter 2: *Human impact on plant biodiversity in the functional floodplain of heavily modified rivers - A comparative study along German Federal Waterways*

The manuscript presents a comparative study of the phytodiversity in the functional floodplain of German Federal Waterways. The objectives were to assess the main drivers of plant species composition and diversity along heavily modified rivers and to show whether natural differences obscure the effects of human alterations. To this end, the vegetation of river banks, grassland and alluvial forest fragments was recorded in 20 study sites (1 km stretches of the functional floodplain of waterways) distributed across Germany. Inferential and multivariate statistics (frequency analyses, non-metric multidimensional scaling, canonical correspondence analyses, regression analyses; see chapter 2.2.4 for detailed descriptions) were applied to identify the main environmental factors that relate to the recorded distribution patterns.

Chapter 3: *Can artificial waterways provide a refuge for floodplain biodiversity? A case study from North Western Germany*

Since canals differ from natural rivers by their origin, their surroundings and especially their low flow velocity, canals were separated from the comparative study (chapter 2) and investigated in a case study to gain first insight in the ecological conditions of canals.

Thus, chapter 3 presents a case study in which the bank vegetation of a canal was compared with the bank vegetation along a river. The objectives were to study how the plant species composition and the plant species diversity of canals differ from those of river banks, which environmental factors are related to these differences, and whether canals can serve as a refuge habitat for endangered floodplain species. To this end, the floristic, functional and structural diversity of the floodplain and the respective adjacent areas of the river Ems and the Dortmund-Ems Canal in North Western Germany were analyzed (applying paired t-tests, non-metric multidimensional scaling, and regression tree analyses, see chapter 3.2.3 for details).

1.4 Main results and conclusions

The two studies of this thesis showed that anthropogenic change in riparian systems causes a shift in species composition. Species adapted to floodplain habitats were replaced by species adapted to terrestrial habitats (chapter 2). This trend was also visible in the banks of the studied canal, but the canal could provide habitats for some endangered riparian and wetland species (chapter 3). Species richness and diversity increased with decreasing naturalness; since disturbance by flooding was limited (or non-existent) and species with less adaptation to floodplain habitats could immigrate into the riparian zone (chapter 2 & 3). To incorporate ecological demands, one possibility for the waterway management could be to aim to reestablish the connection between the river water and the floodplain habitats and to reinstall dynamic conditions as far as possible within the given economic limitations of waterways.

1.4.1 Plant species composition

According to Malanson (1993, p.76), the ecological paradigms for species distribution in natural floodplains are (1) the ecological gradient from terrestrial to aquatic conditions, (2) an intermediate level of disturbance with channel dynamics and flooding as the main disturbing factors, and (3) competition as the driving process for species arrangement along environmental gradients. In anthropogenically impaired riparian systems, these paradigms might not be valid, since the ecological conditions differ substantially from those in natural floodplains. The connection between river and floodplain is interrupted and the flooding regime is altered (e.g. through impoundments, channelization and the resulting deepening of the river channel, or through barrages that regulate the hydraulic regime; Allan and Castillo, 2007, chapter 13). Thus the first aim of this work was to determine which plant species occur in the studied floodplain habitats (question 1), whether endangered floodplain vegetation could be sustained (question 2) and which (anthropogenic) factors were related to plant species distribution (question 4 and 5).

The inventory of plant species diversity in 20 study sites along Federal Waterways showed that floristic composition along the banks and the floodplains differed substantially from the vegetation of unimpaired riparian areas as described by Ellenberg (2009, p.248 ff.). In the studied grasslands, flood meadow species (e.g. *Allium angulosum*, *Silaum silaus*) were rare, while mesophilic grassland species were dominating. The floristic composition was indicative of mesic moisture conditions (Ellenberg, 2009, p.557) and high nutrient loads. Flood meadow species are sensitive to high levels of nutrients, so they occur rarely in

anthropogenically influenced floodplains (e.g. Hölzel & Otte, 2003; Klaus *et al.*, 2011). Sites with high mean Ellenberg Indicator Values for nutrients (Ellenberg *et al.*, 1991) were negatively related to species diversity.

The vegetation of the copse stands under study comprised plant species that reflected the gradient from terrestrial to more aquatic habitats as described by Malanson (1993, p.76). For example, *Salix alba*, a species adapted to frequent flooding, as well as *Acer pseudoplatanus*, a flooding-intolerant species (it can tolerate only up to 4 days of flooding during the vegetation period, Ellenberg & Leuschner, 2010, p. 463), had high frequencies in the sampled stands. Since all sites were located close to the river in the functional floodplain, species composition suggested that altered dynamics and reduced flooding frequencies facilitated the spread of hardwood species in the lower terraces, which was also reported by Van Looy *et al.* (2004) for a Belgian river. The occurrence of *Acer pseudoplatanus* in floodplains is an example for the trend that the zonal woody vegetation of Europe can invade riparian forests if the abiotic conditions are suitable (less frequent flooding, as found by Carbiener and Schnitzler, 1990).

The river banks under study were dominated by biennial and perennial herbs with high demands for moisture and nutrients. Where disturbance events such as flooding and channel shifts were inhibited by embankments, plant species adapted to shallow water zones with low flow velocity prevailed (cf. Ellenberg, 2009, p.250).

The same tendency was visible when the vegetation along the Dortmund-Ems-Canal was compared to the bank vegetation of the river Ems. The analyses showed distinct differences between the less impaired river Ems and the canal. Along the canal, species composition was comparable to that of channelized or modified rivers (see chapter 2, e.g. dominance of *Phragmites australis*). However, numbers of Red List species did not differ significantly between the river and the canal, thus the Dortmund-Ems-Canal could serve as a refuge for single endangered riparian species, as it was the case for some British canals (Willby and Eaton, 1996).

Regional differences in plant species composition played a significant role in the comparative study, but factors related to human influence remained visible (compare the work on several French, Spanish and American rivers by Tabacchi *et al.*, 1996). In both studies (chapter 2 and 3), typical floodplain species were replaced by more common species. Species adapted to wet site conditions or flooding (Ellenberg Indicator Values for moisture, frequent flooding and alternating water levels, Ellenberg *et al.*, 1991) were less frequent along heavily modified rivers or the canal in comparison to the more natural river.

Stress and ruderal strategists (s- and r-strategists, Grime 1979) were declining while competitors (c-strategists) and generalists (csr-strategists) were dominant. For species adapted to high disturbance frequencies, an adaptation to stress and resource limitations is expected e.g. by Nilsson *et al.* (1989), thus a reduction of flooding creates habitats for more common species that can outcompete the specialized floodplain species, as found e.g. by Catford *et al.* (2011) in Australian wetlands. A shift in floristic composition towards more terrestrial species is generally agreed upon when comparing natural and regulated or channelized rivers (see e.g. the review by Poff and Zimmerman, 2010; or Oswalt and King, 2005). The main driving factors are differences in flow regime (mainly magnitude, but also stabilization of high and low flows, reviewed by Poff and Zimmerman, 2010) and frequency of flooding events (Deiller *et al.*, 2001). River embankments and other measures that disrupt the connection between the river channel and the floodplain (e.g. deepening of the river) thus have similar effects (Decamps *et al.*, 1988; Leyer, 2006). These patterns of change in plant species composition are visible - despite natural differences - across regions and have been found even across continents (see also Dynesius *et al.*, 2004).

1.4.2 Floristic and functional diversity

Single natural floodplain habitats are not necessarily rich in plant species (e.g. *Phalaris* or *Phragmites* reeds, Moelder and Schneider, 2011). The high floristic diversity of natural floodplains is attributed to the complexity and dynamics of habitats, which are mainly driven by flooding (Ward, 1998; Ernoult *et al.*, 2006, Naiman *et al.*, 1993). As found in the present investigations concerning plant species distribution, more terrestrial species can colonize anthropogenically influenced or artificially created habitats and thus increase species numbers when these dynamic conditions are reduced. This is in accordance with the results of Deiller *et al.* (2001), who investigated the effects of flooding interruption on alluvial forests. To understand whether the main drivers of plant species distribution along German Federal Waterways also played a role for floristic richness and diversity, the main factors related to different biodiversity indices were analyzed (question 4). Further, it was of special interest whether natural regional differences were of importance and whether the effects of anthropogenic influence remained visible despite these differences (question 5). In both studies (chapter 2 and 3) higher species numbers and diversity indices were related to areas with stronger human influence. Along the canal, diversity was always higher than along the Ems. Also Willby *et al.* (2001) and Willby and Eaton (1996) found that phytodiversity was high along canals. In the present study comparing rivers under human

influence (chapter 2), especially bank protection was related to high values for diversity indices, while shipping traffic and regulation by barrages were negatively related, which was also the case in studies by Willby and Eaton (1996), Dynesius *et al.* (2004) and Jansson *et al.* (2000).

Alteration of the flooding regime (e.g. by barrages) was identified as one of the main drivers for changes in floristic composition (see chapter 1.4.1). In relation to biodiversity measures, different studies report that a reduction of flooding and thus disturbance can have diverse effects. While Deiller *et al.* (2001) report an increase in plant species diversity with reduction of flooding, Chipps *et al.* (2006) and Poff and Zimmerman (2010) show that anthropogenic alterations of flooding regimes decrease floral and faunal species diversity. Deiller *et al.* (2001) found that the increase in plant species richness was caused by the introduction of flooding-intolerant species into the system, which corresponds to the results for species composition reported above. Many researchers state that floodplain biodiversity is highest at intermediate levels of disturbance, thus applying the intermediate disturbance hypothesis (IDH) by Connell (1979; Lite *et al.*, 2005; Pollock *et al.*, 1998; Tabacchi *et al.*, 1996). In this context, Ward *et al.* (1999) emphasize that diverse disturbance regimes maximize biodiversity. With increasing distance from the river channel, disturbance by flooding decreases, thus increasing the number of coexisting successional stages along the disturbance gradient (Ward *et al.*, 1999). However, when testing for the IDH experimentally, Amoros and Bornette (1999) did not find clear evidence. Anyhow, the disturbance of riparian systems by human actions actually decreases the (natural) disturbance of floodplain habitats by frequent flooding. Thus, when considering the IDH, these two terms (human vs. natural disturbance) should be clearly differentiated.

Next to the alterations directly affecting the river morphology and hydrology, changes in land use and landscape structure are anthropogenic disturbances that showed strong relations to biodiversity in all systems under study. Méndez-Toribio *et al.* (2014) and Allan (2004) related this to the influence of negative edge effects such as pesticide runoff from agriculture and elevated nutrient levels, which was also visible in the compositional changes in grassland and the high Ellenberg Indicator Values for nutrients (chapter 2). While these effects cause a decrease in species diversity, a higher land use differentiation might increase the species pool of the landscape (Liu *et al.*, 2013). Similarly, landscape structural diversity (reflected in a high edge density) was related to high species diversity indices along the Dortmund-Ems-Canal (chapter 3). Also Kumar *et al.* (2006) identified edge density within a small buffer radius as an important driver for species diversity. When

considering the canal as an artificial waterway, Bolpagni *et al.* (2013) point out that for lower or higher levels of species diversity it is less important whether a water body is of natural or artificial origin than whether it is structurally rather uniform or heterogeneous.

The case study along the Dortmund-Ems-Canal further provided the opportunity to study the relation between measures of plant species diversity and measures of plant functional diversity and the differences in functional diversity between a river and a canal (question 3). The results for functional richness and evenness did not correspond to those of species diversity, which is plausible since functional redundancy can buffer losses in species diversity (Mayfield *et al.*, 2010). Functional divergence was significantly higher along the river Ems than along the canal. This measure is related to a higher degree of niche differentiation and a higher number of specialized plant species (Kotowski *et al.*, 2013), which is confirmed by the results for species composition. Even though the influence of the calculated functional diversity measures on ecosystem functionality was not explicitly studied in this thesis, it is recommended to consider functional divergence in conservation planning since it is known to be related to competition, a driver of ecosystem functions (Kotowski *et al.*, 2013). Moreover, restoration of the functional composition of endangered (floodplain) habitats can be more feasible than the restoration of the original species diversity (Woodcock *et al.*, 2011). Therefore, for the evaluation of floodplain functionality, not only species numbers and diversity metrics, but composition and functional groups on the community level need to be considered.

1.4.3 Implications for management

Since the results obtained in this study gave insight into the influence of human activities along waterways, several implications for the incorporation of biodiversity demands into the management regime could be developed (question 6).

For rivers under strong economic pressure such as waterways, a complete restoration is neither possible nor viable (Naiman *et al.*, 1993; Ward *et al.*, 2002). Thus, White and Stromberg (2011) recommend defining feasible restoration goals within the given limitations.

Generally, restoration should be system-wide and not be pointed at single species groups (Naiman *et al.*, 1993), and it should be process-oriented, i.e. directed at stream hydrology (Nilsson, 1992). In accordance, those measures that simulate natural conditions have proven the most successful (Naiman and Decamps, 1997). For instance, an alteration of the flooding regime towards a more natural system might increase floodplain diversity

(Naiman and Turner, 2000). Even within limitations, this might be achievable by recurrent (controlled) floods, which have been proven to have a high restoration potential (Alfredsen *et al.*, 2012; Allan and Castillo, 2007). Ward *et al.* (2002) suggest that a moderate increase of dynamics even in intensively managed riparian systems might increase the river – floodplain connectivity. In general, all measures reconnecting the elements of the riparian landscape (e.g. by removal of impoundments) are beneficial (Allan and Castillo, 2007; Nilsson, 1992).

On a landscape perspective, the reintroduction of fluvial dynamics should lead to a diversification of habitats and thus increase diversity on the ecosystem/landscape scale (Naiman and Turner, 2000). To allow for this, the provision of habitat space is needed. In this context, Rösch *et al.* (2015) report that for the conservation of species diversity (across several taxa, in their case studied in calcareous grassland), the availability of many small habitat fragments as well as single large fragments is of importance, which is an aspect that should be considered in restoration management. Intensive land use has negative influences on the biodiversity of floodplains, not only because of the loss of habitat space for floodplain communities, but also because of the high amount of nutrient and pesticide runoff (Méndez-Toribio *et al.*, 2014). Since high nutrient levels are negatively related to the occurrence of floodplain meadow species (Mathar *et al.*, 2015), and plant species richness in wetlands is related to low soil phosphorous content as found by Audet *et al.* (2015), it is viable to consider soil nutrient levels in restoration projects.

However, the finding that species numbers were increased in highly impaired floodplains implies that restoration measures aimed to increase ecosystem functionality could lead to a decrease in species diversity (Deiller *et al.*, 2001), at least on the short term. This might be acceptable since more natural habitat types and typical (and in many cases endangered) floodplain species would be promoted, as it was the case in an Austrian restoration project (Funk *et al.*, 2013). For the incorporation of conservational demands in the management of German Federal Waterways, the aforementioned conflict between species numbers and naturalness needs to be acknowledged.

In accordance to these considerations, the European Habitats Directive (The Council of the European Communities, 1992) recommends to maintain the natural dynamics in the hydraulic situation of rivers (Ssymanck *et al.*, 1998). Therefore anthropogenic modifications of hydraulic conditions are included in the reference list of Threats, Pressures and Activities (DG Environment, 2011). The Habitats Directive (The Council of the European Communities, 1992) includes the protection of floodplain habitats (e.g. *Cnidion dubii*

meadows (type 6440), hydrophilous tall herb fringe communities (type 6430), or alluvial forests (type 91E0)) and natural or semi-natural rivers (e.g. water courses with *Ranunculus fluitantis* vegetation, type 3260) themselves, thus their protection and restoration is of legal concern.

Canals as artificial waterways cannot reach a status comparable to natural rivers. However, Article 1f) and 1i) of the Habitats Directive (The Council of the European Communities, 1992) define a habitat as an environment in which a species lives “at any stage of its biological cycle” and state that if a habitat is large enough to sustain a population, its conservation status can be defined as “favourable”. Therefore a canal can reach a positive conservation status if it provides space for endangered species or habitat types. Moreover, the Habitats Directive explicitly lists linear structures like riparian systems - or canals - as essential for the dispersal and migration of wildlife (article 10) and consequently asks to improve the status of ecologically important landscape features (The Council of the European Communities, 1992), which applies to artificial as well as natural waterways.

In Germany, 50 % of the floodplains are located in NATURA 2000 areas (Brunotte *et al.*, 2009). However, the implementation of the directive has been subject to conflicts and debates due to competing interests of economy, policy and science (Gibbs *et al.*, 2007). The Habitats Directive asks to avoid further deterioration, but when new projects are planned, the directive allows recognizing “overriding public interest” over nature conservation needs (article 6, The Council of the European Communities, 1992). Thus, the implementation of the Habitats Directive in economically important riparian areas is subject to disagreements.

In an exemplary conflict situation between the Habitats Directive and economic demands in an estuary in Great Britain, Gibbs *et al.* (2007) describe an approach considering new concepts in ecology. Instead of aiming at the restoration of a natural state of the system, this concept acknowledges that nature and humans interact and humans form landscapes by their actions. They seek to preserve the system including its dynamics and its functions (Gibbs *et al.*, 2007) instead of returning to a strictly historical natural state, which is often not viable.

A comparable concept applies for canals. These can be considered as man-made, novel ecosystems *sensu* Hobbs *et al.* (2006), which cannot be changed back to a natural state. Therefore, their intrinsic value should be recognized and management should focus on functional diversity (Callow, 2012; Tilman *et al.*, 1997; Woodcock *et al.*, 2011) and their ecosystem services (Hobbs *et al.*, 2006; Hobbs *et al.*, 2009). The results of the case study

showed that the Dortmund-Ems-Canal can provide habitat space for endangered riparian species; hence the habitat function should come in the focus of its management.

Since canals do not allow for an increase of dynamics, measures applied to riparian systems are inappropriate. Allowing for a moderate amount of natural succession along the banks by implementing a scheme of ‘benign neglect’ as recommended by Chester and Robson (2013) might increase structural longitudinal heterogeneity and therefore enhance the ecological value of the banks of artificial canals.

To increase the ecological status and biodiversity of German Federal Waterways, both nature conservation and economic demands need to be acknowledged. The often contrasting interests need to be taken into account and compromises need to be found. To improve communication between stakeholders and to increase the acceptance of restoration efforts, more distinct definitions and targets than just ‘enhancing biodiversity’ are required since different species groups react differently and different goals require different management options (Findley *et al.*, 2002). As the results of this thesis have shown, system-oriented measures can in some cases decrease ‘biodiversity’ (in that case plant species richness, often used synonymously for biodiversity, as stated e.g. by Kempton, 2002) on the short term, which may cause misunderstandings and conflicts (Funk *et al.*, 2013). Therefore, an incorporation of biodiversity demands in waterway management depends on a clear definition of indicators used to describe biodiversity in a riparian context.

1.4.4 Conclusions and perspectives

The results of this thesis showed that the bank and floodplain vegetation of riparian systems under strong anthropogenic pressure was mainly composed of species adapted to terrestrial site conditions. Thus the floristic patterns reflected the abiotic changes caused by human alterations, namely those that affect the hydraulic connections between the river channel and the floodplain and, more specifically, those that inhibit flooding. Due to the altered disturbance regime, less specialized plant species could develop in the riparian zone and outcompete typical floodplain species. Therefore, increased levels of anthropogenic influence and decreased naturalness of the studied areas led to increased plant species richness. These patterns remained visible despite regional differences between the study sites.

The studied indicators for floristic diversity, namely plant species composition, species richness, species evenness, species diversity, functional diversity and habitat diversity,

reacted differently to human alterations. Rivers with a higher level of construction and the canal showed high species numbers, higher evenness and diversity, but species were less specialized, as also shown by the lower functional divergence along the canal. In the comparative study, protected floodplain species occurred mainly along the less impaired rivers. The habitat structure was homogenized and the ecological value of the habitats was low. For the incorporation of ecological demands in waterway management, measures should aim to reinstall dynamic hydrological situations and to increase flooding magnitude and frequency. Thus the natural dynamic habitat conditions could be restored as far as possible within the given economic limitations. While these measures could promote typical and endangered floodplain plant species, total species numbers might decrease on the short term.

This raises the question which indicators for biodiversity should be in the focus when discussing the conservation or restoration of floodplains as diversity hotspots. The analyses in this work indicate that a high floristic diversity, in this case defined as plant species richness and diversity on the community level, might even be related to a decreasing naturalness (reflected by species and habitat composition) of the systems under consideration. Species composition and functional diversity might be better indicators since they are related to the differentiation of ecological niches. Similarly, Noss (1990) points out that qualitative change in the structure of a community is a better indicator for ecological disturbance than quantitative indices. For the restoration of floodplain meadows, Woodcock *et al.* (2011) could show that the restoration of the composition of functional groups could be achieved on a much shorter time scale than the restoration of the original species composition. Thus, the functional diversity approach is worth to be taken into consideration in further research on this topic. Furthermore, when comparing different systems across regions, functional diversity might be a better indicator than species' compositional indicators, since some species do not occur in all regions, and their trait space might be covered by other species with a different geographical distribution range. Therefore, it would be valuable to further investigate the functional diversity along waterways.

In this work, a set of indicators was analyzed (as recommended e.g. by Magurran and McGill, 2011, p.292 *ff.*) for a holistic assessment of the phytodiversity along German Federal Waterways on community and ecosystem level, i.e. species composition, species richness, Shannon and Simpson index, species characteristics, endangered species in chapter 2 and additionally functional diversity and habitat diversity in chapter 3. Since

these measures did not always correspond to each other, and the conducted wide assessment was demanding, the task for further research might be to find few, easily applicable indicators that are sensitive towards the impact factors in question. Thus, not only the disturbance of natural systems, but also the success of restoration measures could be assessed more quickly and legislative goals that ask for ‘protection of biodiversity’ could be further refined. “This ability to be multifaceted while not losing sight of the basic storyline must be how we approach the measurement of biodiversity going forward when all eyes of society are on us” (Magurran and McGill, 2011, p. 293).

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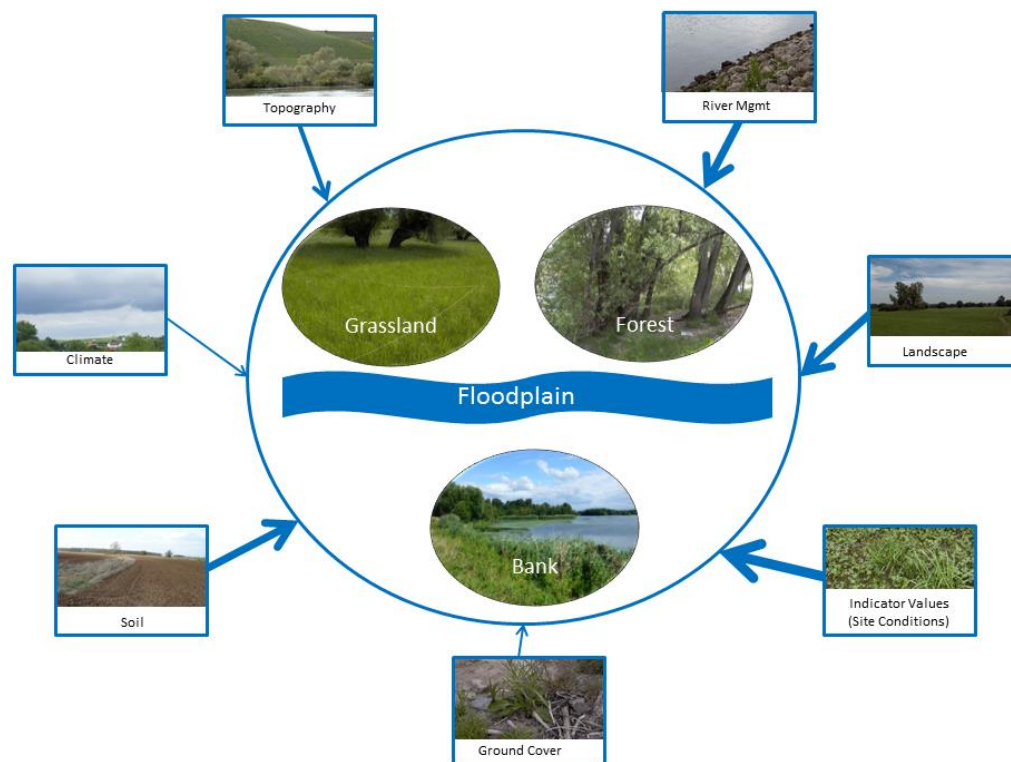
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Chapter 2

Human impact on plant biodiversity in functional floodplains of heavily modified rivers - A comparative study along German Federal Waterways

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Abstract

Rivers and their floodplains have been strongly influenced by human actions, such as river training measures, flow regulation, bank stabilization, or intensive land use. These alterations threaten the biodiversity of floodplains. While the effects of individual factors on plant species composition and diversity in riparian systems have been frequently studied, it is yet unknown how multiple stressors act in concert and whether the effects remain visible across regions.

We chose the floodplains of German Federal waterways (rivers with a high frequency of shipping traffic) to study the main drivers of plant species composition and biodiversity along heavily modified rivers and aimed to show whether natural differences obscure the effects of human alterations. We recorded the vegetation of river banks, grassland and alluvial forest fragments in 20 study sites distributed across Germany.

Species composition differed from natural floodplain alliances and showed a trend towards terrestrialization and an increase of common species that show no specific preference for floodplain habitats. Despite natural differences such as topography and climate having the strongest influence on plant composition and diversity, the effects of anthropogenic influence (e.g. land use, shipping traffic) remained visible. River construction tended to increase species diversity since the terrestrial species pool is bigger than the one of floodplain specialists. For restoration and ecological river management not only species numbers but their composition and ecological specifics should be considered, and local conditions need to be taken into account.

2.1 Introduction

The large rivers and streams of temperate regions have been severely altered by human actions (Giller & Malmqvist, 1998). Rivers and their floodplains are – in their natural state - among the most species-rich ecosystems. Therefore they are especially sensitive to alterations, which indeed have led to the deterioration of these ecosystems worldwide (Funk *et al.*, 2013; Malanson, 1993; Tockner & Stanford, 2002). In Germany, 90% of the floodplains are degraded by human action (Brunotte *et al.*, 2009) and similar numbers apply to European and North American riparian areas (Tockner & Stanford, 2002). Especially navigable waterways, which are used for shipping traffic, are highly modified (Wolter, 2001).

Since the protection of riparian habitats has received increasing attention in international policy, e.g. in the European Habitats Directive (92/43/EEC, The Council of the European Communities, 1992), the Convention on Biodiversity (CBD, United Nations, 1992), the Millennium Ecosystem Assessment (MEA, 2005) and the European Water Framework Directive (2000/60/EC, European Community, 2000), also heavily modified rivers such as waterways came in the focus of biodiversity research (e.g. Pataki *et al.*, 2013). As human interventions are inevitable to maintain the infrastructure of waterways, construction measures that consider ecological conservation issues are recommended (Wolter, 2001; Pataki *et al.*, 2013). Anthropogenic modifications of rivers and riverscapes are diverse (Allan, 2004). The most important forms of river regulation are modification of river dynamics, river dredging, straightening of the river channel, stabilization of banks and building of artificial levees (Deiller *et al.*, 2001; Van Looy *et al.*, 2004; Ward, 1998).

River regulation and channelization lead to a shift in species composition (Baart *et al.*, 2013) and to a decrease in species numbers (Franklin *et al.*, 2001; Jansson *et al.*, 2000; Nilsson *et al.*, 1991; Uowolo *et al.*, 2005). This decrease in species richness has been studied frequently and is valid across continents (Dynesius *et al.*, 2004). Poff & Zimmermann (2010) reviewed 165 papers on the ecological effects of flow alterations, of which 92% reported decreases in ecological response parameters (e.g. species numbers).

When considering human influences on ecosystems, land-use changes such as deforestation, urbanization, or especially the intensification of agricultural land use, are seen as the main driver for biodiversity loss (Sala *et al.*, 2000; Waldhardt, 2003). This seems to be true also in floodplains (Donath *et al.*, 2015; Härdtle *et al.*, 2006; Méndez-Toribio *et al.*, 2014). In an earlier case study on the diversity of plants along the banks of a canal in comparison to those of a river (Harvolk *et al.*, 2014), we found that land use

patterns and landscape structure were related to biodiversity distribution along both systems under study. In that context, Méndez-Toribio *et al.* (2014) explain that intensive land use causes negative edge effects like pesticide runoff, which negatively influence species richness. In contrast, diverse land use and landscape structure patterns may increase the species pool at the landscape level (Liu *et al.*, 2013).

In total, the distribution patterns of vegetation are influenced by factors operating on the local and on the regional scale; they are driven by natural as well as anthropogenic disturbance (Ward, 1998). However, the relative importance of natural regional differences compared to anthropogenic effects still remains unknown.

Studies on the effects of anthropogenic alterations of rivers and their closest surroundings were mostly case studies along single riparian systems (Banasova *et al.*, 2004; Härdtle *et al.*, 2006; Hupp *et al.*, 2009; Martins *et al.*, 2013). Since every river system is unique in respect to the aforementioned natural disturbance (e.g. hydraulic regime or microtopography), generalizations are difficult (Bendix & Hupp, 2000; Giller & Malmqvist, 1998). In addition, very few studies analyzed human impacts on ecosystems across regions (Douda, 2010; Dynesius *et al.*, 2004). However, they focused on only one single aspect of anthropogenic disturbance, like regulation (Nilsson & Berggren, 2000; Nilsson & Jansson, 1995), channelization (Franklin *et al.*, 2001), or river embankment (van Looy *et al.*, 2004). While these singled-out effects of human impacts are well-studied, it remains unclear how strongly each of them influences species distribution and biodiversity when multiple stressors are affecting the system, and whether those patterns remain visible across regions (but see Tabacchi *et al.*, 1996).

Consequently, Bendix & Hupp (2000) ask for a multidimensional context when investigating the influence of different-scale variables on floodplain vegetation. In accordance, we are interested in the influence of different types of human interventions on plant species distribution across several different riparian systems, and whether natural differences between systems (e.g. geographic, climatic, topographic) mask these effects. To this end we have assessed the floodplain vegetation in 20 study areas along German Federal Waterways that are used for shipping traffic. The German Federal Waterways serve as a good example to study effects of river regulation, construction and maintenance since they are managed by one administration, following similar regulations (WaStrG, 2013). Our study sites differed in regulation, bank protection, traffic intensity and surrounding land use, and they were evenly distributed across Germany, thus covering a

gradient of continentality and elevation. With this set of study areas we aim to answer the following questions:

- 1) Which plant species are found in alluvial forests, flood meadows and the bank vegetation along rivers under high anthropogenic pressure?
- 2) How do these habitats differ from ‘natural’ riparian habitats and do they provide space for endangered floodplain species?
- 3) Which are the main driving factors for species composition and species diversity?
- 4) How strongly does river management influence species composition and diversity compared to natural driving factors?

2.2 Materials and Methods

2.2.1 Study sites

German Federal Waterways are navigable surface waters under state administration. They make up 29.8% of the German surface waters (total length: 6900 km). 77% of them are rivers and streams, 23% are artificial canals (Wolter, 2001). Our study comprised twenty study sites that were selected from the total of the German Federal Waterways, applying a stratified random scheme to achieve an even distribution across all waterways. We a priori classified the rivers and streams according to a grouping into ‘mountainous areas’ vs. ‘plains’ (Koenzen, 2005), ‘steep longitudinal slopes’ ($> 0.5\text{‰}$ inclination) vs. ‘flat slopes’ ($\leq 0.5\text{‰}$ inclination) (Koenzen, 2005), and ‘regulated’ (by barrages or other transversal structures) vs. ‘free-flowing’ (BMVBS, 2009). The classification resulted in 5 classes, which are summarized in tab.2-1.

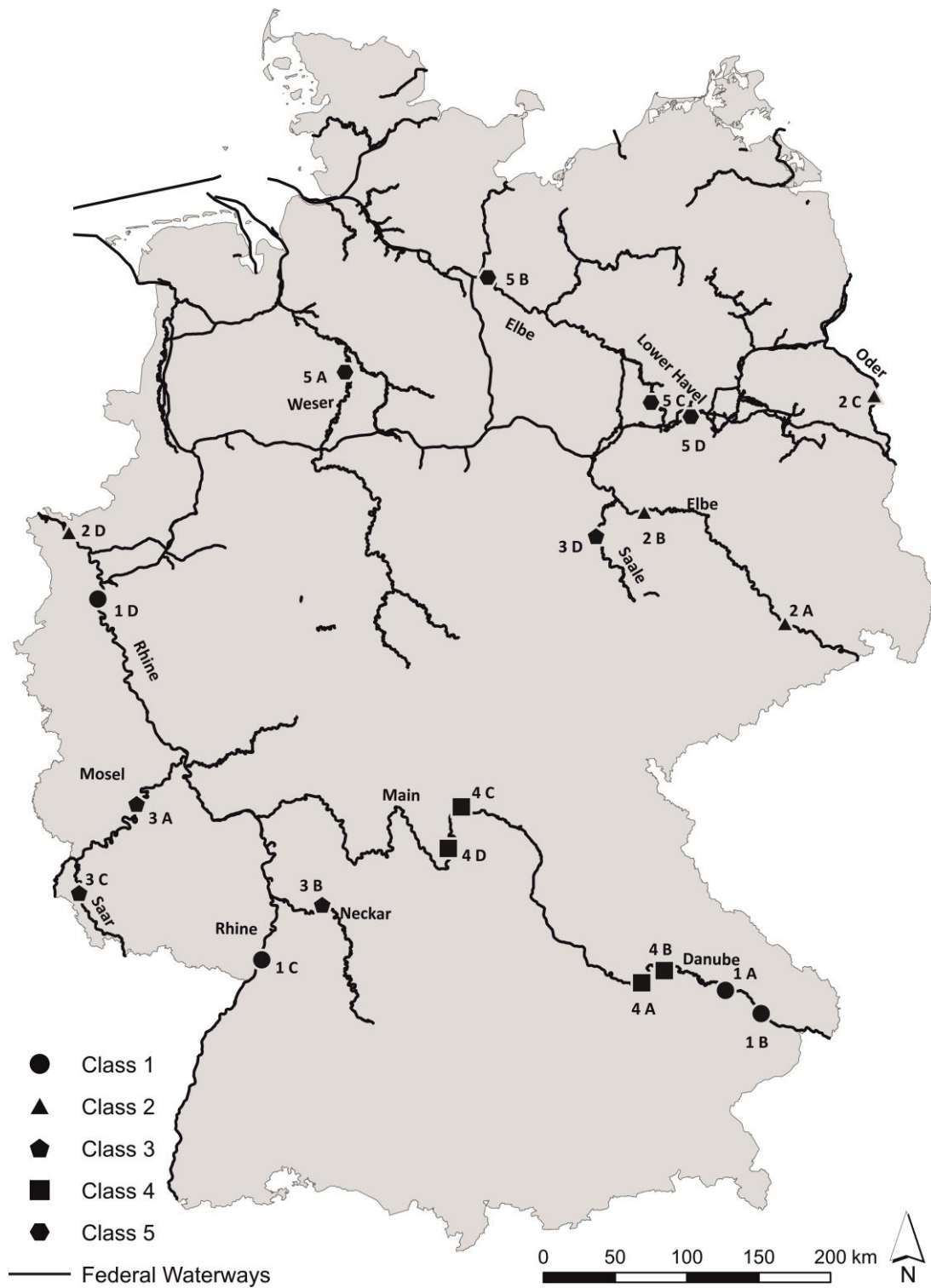
Table 2-1: Classification of German Federal Waterways for stratified random selection

Class	Landscape	Inclination	Regulation
1	mountainous	$\leq 0.5\text{‰}$	free-flowing
2	plains	$\leq 0.5\text{‰}$	free-flowing
3	mountainous	$> 0.5\text{‰}$	regulated
4	mountainous	$\leq 0.5\text{‰}$	regulated
5	plains	$\leq 0.5\text{‰}$	regulated

Within each class, we randomly selected 4 study sites (see fig. 2-1) from a total of 11 rivers (Danube: 4 sites; Rhine, Elbe: 3 sites; Main, Lower Havel: 2 sites; Oder, Mosel, Neckar, Saar, Saale, Weser: 1 site).

Canals were excluded from the present study since their species composition differs substantially from that of natural rivers (cf. Harvolk *et al.*, 2014). Similarly, we excluded waterways with less than 1 Mio tons of transported goods per year (WSV, 2013), as these rivers are of minor importance for traffic and are thus less intensely managed. Since we were interested in the ‘normal landscape’ without further influence of settlements or nature conservation measures, river stretches within settlements or within nature conservation areas were excluded. This left 19.5% of the total waterway length for selection.

A study site covered 1 km of floodplain length along the respective river and the extent of the functional floodplain (Brunotte *et al.*, 2009), thus the 20 study sites differed in size (from 9.6 hectares to 333.4 hectares). The functional floodplain is defined as the area directly inundated by the river at high water levels, while the fossil floodplain is not directly inundated anymore, mainly due to the construction of levees (Leyer, 2004). Classification and random selection was based on the official Federal waterway map (BMVBS, 2009) and conducted in ESRI ArcGIS 10 (ESRI, Redlands, CA, USA) using the Hawth's Tools Extension (Beyer, 2004).



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Data source: German Federal Waterway Network, Version 1.1, provided by the BfG

Figure 2-1: Overview of the German Federal Waterways and the location of the study sites. Numbers indicate classification of the sites (see tab. 2-1).

2.2.2 Vegetation Sampling

We sampled the vegetation once in early summer 2013 or 2014 (May to July). In 2013 sampling was interrupted by the extreme flood along the Danube and Elbe catchments (Merz *et al.*, 2014) and was continued in 2014. The possible effect of this severe event was taken into account by including the sampling year in the statistical analyses. The cover of each vascular plant species was estimated using an ordinal scale from 1-9 (van der Maarel, 1979). For each study site, we recorded 6 relevés in grasslands (25 m²; Westhoff & van der Maarel 1973), 6 relevés in alluvial forest fragments (hereafter referred to as ‘copse’; 100 m², Westhoff & van der Maarel 1973), and 4 to 8 relevés along the river banks, depending on accessibility. Those were divided into 3 sub-relevés with increasing distance from the water, each 1 x 4 m in size, since long and narrow plots are more suitable for the detection of rare species in riparian habitats (Dynesius *et al.*, 2004). There were no significant differences between those sub-relevés, thus they were merged for further analyses. We used the average percentage of cover values which was then transformed into ordinal scale following Van der Maarel (1979).

The grassland and copse relevés were randomly selected within the respective habitat types. The bank relevés were located in a regular scheme every 200 meters along the river banks. Since not every study site included both grassland and copse habitats, we sampled a total number of 96 grassland relevés, 114 copse relevés and 116 bank relevés. We followed the nomenclature of Wisskirchen & Haeupler (1998).

2.2.3 Predictor variables

During sampling in the field, we recorded the coordinates of each relevé, the height above sea level, slope and aspect, cover and mean height of tree, shrub and herb layer, as well as the cover of moss, litter, open water and open soil. The responsible waterway authorities were questioned to gain information on bank protection, management, and regular maintenance along the respective river stretches. Maintenance always followed the same regime, that is regular cutting of shrubs and trees only if they endanger shipping traffic, mowing of the river banks around traffic signs to ensure readability, and maintenance of the bank protection. Therefore, we could not determine different categories of management. Information on the regulation, the state of construction and the waterway class (a classification of waterways used by the waterways authorities based on their size, depth, and shipping traffic) of the respective rivers was obtained from the official Federal

waterways map (BMVBS, 2009). To account for floodplain losses, we calculated the relation between the functional floodplain and the historical floodplain, based on the German floodplain inventory (Brunotte *et al.*, 2009).

To gain insight into landscape structure, the biotope types of the study sites were mapped using the biotope type key of the German Federal Institute of Hydrology (BfG, 2003). We calculated the distance to the river channel for each relevé, the Shannon's diversity index for landscape structure and the edge density [meters/hectares] from the resulting biotope type maps in ArcGIS using the vLate extension (Lang & Tiede 2003). We followed the definitions given by Lang & Blaschke (2007). From a Digital Landscape Model 1:25,000 of the German Official Topographic Cartographic Information System (ATKIS-DLM 25, provided by the German Federal Institute of Hydrology), we calculated the amounts of the land use classes arable land, grassland, forest and settlement for our study sites and for a surrounding buffer of 1 kilometer, to account for land use intensity.

Climate data was obtained from the German Meteorological Service (DWD, 2013). We analyzed the soil map for Germany (BÜK1000, BGR, 2013), and we extracted information on climate zone, soil geographic region, soil landscape, dominating soil types, and acidity (from proportion of area covered by calcareous substrate).

We used cover weighted Ellenberg indicator values (hereafter: EIV, Ellenberg *et al.*, 1991) as a surrogate for local site conditions which could not be measured in a satisfactory way in the field. Field measures tend to be a snapshot of the local situations in time (Zelený & Schaffers, 2012), especially when it comes to factors like soil moisture which is highly variable over short periods of time. Thus, EIVs are a suitable proxy for site conditions (Diekmann, 2003; Zelený & Schaffers, 2012).

All input variables and their factor levels are summarized in tab. 2-A1 in the appendix.

2.2.4 Statistical Analyses

For species composition, we inspected in detail the traits of species with the highest occurrences in all habitat types. We assumed that species occurring in floodplains with a natural flooding regime mainly follow a stress or ruderal strategy (Grime, 1979), while species adapted to terrestrial habitats without regular flooding are mainly competitors (as found by Pautou & Arens, 1994). We further assumed that floodplain species are adapted to high moisture levels, frequent flooding or alternating water levels, as reflected in the EIV for moisture (Ellenberg *et al.*, 1991). Thus we analyzed the strategy types (CSR;

Grime, 1979) and the Ellenberg moisture (EM) values of the most frequent species. EM and CSR values were derived from the BIOLFLOR database (Klotz *et al.*, 2002). We further inspected the occurrence of Red List species (Red List of Germany; Ludwig & Schnittler, 1996), their strategy types and moisture values.

To account for differences in habitat conditions and in relevé size, all analyses were performed separately for the grassland, copse and bank datasets.

Prior to multivariate explorative analyses, species that occurred less than two times were omitted from the datasets to avoid masking of effects (Leyer & Wesche, 2007). We investigated patterns in species distribution by applying non-metric multidimensional scaling (NMS). We used the Sørensen distance measure (Bray-Curtis distance), two dimensions, 50 iterations and starting configuration by random number. NMS was performed using the software package PC-ORD 5.32 (McCune & Grace, 2002).

To determine the magnitude of the effects of predictor variables on species composition, we performed a series of partial Canonical Correspondence Analyses (CCA) with rare species downweighted in CANOCO 5 (Microcomputer Power Co., Ithaca, New York, USA; Ter Braak & Smilauer, 2012). Significance of relationships between CCA axes and species composition was tested by Monte Carlo permutation (Ter Braak, 1987).

To produce variance components that are ecologically interpretable in variance partitioning, we grouped our predictor variables into the following sets (ref. tab. 2-A1): topography, climate, ground cover, river, river management, landscape characteristics, EIVs, and soil characteristics. We used the coordinates of our plots to construct nine spatial variables that formed the terms of a cubic trend-surface polynomial (Borcard *et al.*, 1992) to account for spatial autocorrelation in our data. The initial dataset with 46 variables comprised redundant information, thus the number of environmental variables was reduced by applying forward selection in CANOCO (Palmer, 1993). The remaining spatial components were always included as covariates to account for spatial autocorrelation (Jongman *et al.*, 1995). To differentiate between the gross and net effects of the groups of environmental variables on species composition, we first quantified the gross effects by performing a series of CCAs (with spatial components as covariables) for each group of variables. To determine the net effect of each set of variables, we performed a series of partial CCAs, controlling for all other variables (Okland & Eilertsen, 1994).

We calculated the species diversity measures richness, Shannon index (Shannon and Weaver, 1963), and evenness (Hill, 1973) by applying the algorithms implemented in the software Turboveg (Hennekens & Schaminée, 2001).

To determine the relative importance of the explanatory variables for species richness, Shannon diversity and evenness, we used General Regression Models (GRM) in Statistica 12 (Statsoft Inc., Tulsa, OK, USA). Variables were Box-Cox-transformed prior to analysis to enhance homogeneity of variance. We included the same explanatory variables as in the CCA analysis plus mean height and cover of the vegetation layers in a multivariate GRM, using forward regression and Wilks Lambda, with the response variables species richness, Shannon diversity and evenness. Subsequently, we performed separate univariate GRMs for each response variable, using stepwise-forward regression. We calculated estimates of variance explained (EV in %), which is the ratio of sums of squares of each significant variable to the total sum of squares in the model (Simmering *et al.*, 2006). In the bank dataset, two cases were excluded as outliers. Grassland and copse datasets did not show any outliers.

2.3 Results

2.3.1 Species composition

We recorded 309 plant species in the bank relevés (n=116), 220 species in the grassland relevés (n=96) and 258 species in the copse relevés (n=114; cf. chapter 3.2). Species that were equally distributed across all habitat types were mainly graminoids that are adapted to mesic moisture conditions, such as *Dactylis glomerata*, *Elymus repens* or *Poa trivialis* (tab. 2-2). While species adapted to alternating water levels were found in all habitat types, species indicative for frequent flooding were restricted to the bank and copse habitats. Other species that occurred frequently were common species like *Urtica dioica* and *Glechoma hederacea*, which indicate high nutrient availability (Ellenberg nutrient values 8 and 7, respectively), but also *Phalaris arundinacea*, which requires moist site conditions and alternating water levels. These were also the species with the highest constancy in the bank relevés, followed by *Rubus caesius* and *Galium aparine*. The banks were dominated by C-strategists that are adapted to high moisture levels (26% with EIV for moisture of 7 or higher or indicating alternating water levels or flooding, tab. 2). Biennial (*Chaerophyllum bulbosum*) and perennial forbs (*Urtica dioica*, *Artemisia vulgaris*) and other species of the Galio-Urticenea were frequent.

Most species that were recorded frequently in the grassland relevés are graminoids such as *Alopecurus pratensis*, *Arrhenatherum elatius*, *Festuca sp.* or *Poa sp.*, or typical grassland

forbs such as *Trifolium sp.*, *Plantago lanceolata* or *Rumex acetosa*. Species of the *Cnidion* or *Molinion* alliances were rare or absent (compare tab. 2-3).

In the copse relevés, tree and shrub species (*Salix sp.*, *Acer pseudoplatanus*, *Crataegus monogyna*) occurred frequently. The understory was mostly dominated by *Urtica dioica*, and other typical shrub, forb and graminoid species of alluvial forests (e.g. *Humulus lupulus*, *Crataegus monogyna*, *Galium aparine*, *Glechoma hederacea*, *Dactylis glomerata*). In general, copse relevés differed much less in terms of species composition among study sites compared with the other two habitat types (fig. 2-2).

Table 2-2: Species with highest frequencies in the respective habitats. All species which occurred in 20% or more relevés in one of the habitats are reported. Species are attributed to one habitat type if their frequency in this habitat is at least 10% higher than in any of the other habitat types. All species with less than 10% difference in frequency are listed as 'equally frequent'. EM = Ellenberg moisture value (Ellenberg et al., 1991); ~ indicates adaptation to alternating water levels; = indicates adaptation to regular flooding; CSR = ecological strategy types according to Grime (1979); C = competitor, S = stress strategist, R = ruderal strategist.

	Species	EM	CSR	Appears in % of records		
				Bank	Copse	Grassland
Bank	<i>Carex acuta</i>	9 =	cs	30	5	0
	<i>Cirsium arvense</i>	x	c	23	8	13
	<i>Lythrum salicaria</i>	8 ~	cs	22	5	1
	<i>Phalaris arundinacea</i>	8 ~	c	52	32	22
	<i>Phragmites australis</i>	10	cs	27	16	0
	<i>Solidago gigantea</i>	6	c	22	11	0
Copse	<i>Acer pseudoplatanus</i>	6	c	3	25	0
	<i>Alliaria petiolata</i>	5	cr	7	25	1
	<i>Cornus sanguinea</i>	5	c	7	27	0
	<i>Crataegus monogyna</i>	4	c	10	39	0
	<i>Fraxinus excelsior</i>	x	c	8	29	0
	<i>Galium aparine</i>	x	cr	36	64	14
	<i>Geum urbanum</i>	5	csr	7	27	0
	<i>Humulus lupulus</i>	8 =	c	15	25	0
	<i>Ranunculus ficaria</i>	6	csr	18	32	10
	<i>Rosa canina</i>	4	c	3	23	0
	<i>Salix alba</i>	8 =	c	14	40	0
	<i>Sambucus nigra</i>	5	c	2	25	0

Table 2-2 (continued)

Grassland	<i>Achillea millefolium</i>	4	c	17	4	28
	<i>Alopecurus pratensis</i>	6	c	23	16	64
	<i>Arrhenatherum elatius</i>	5	c	28	13	45
	<i>Festuca pratensis</i>	6	c	7	4	35
	<i>Festuca rubra</i>	6	c	9	3	21
	<i>Galium album</i>	5	c	10	4	25
	<i>Holcus lanatus</i>	6	c	10	8	26
	<i>Plantago lanceolata</i>	x	csr	24	6	40
	<i>Poa pratensis</i>	5	c	13	2	29
	<i>Rumex acetosa</i>	x	c	9	3	27
	<i>Taraxacum Sec. Ruderalia</i>	5	csr	33	17	44
	<i>Trifolium dubium</i>	4	r	6	1	24
	<i>Trifolium pratense</i>	5	c	8	1	36
	<i>Trifolium repens</i>	5	csr	12	2	23
	<i>Vicia sepium</i>	5	c	11	2	26
equally frequent	<i>Agrostis stolonifera</i>	7 ~	csr	22	24	13
	<i>Calystegia sepium</i>	6	c	33	25	3
	<i>Chaerophyllum bulbosum</i>	7	c	22	22	7
	<i>Dactylis glomerata</i>	5	c	46	32	57
	<i>Elymus repens</i>	x ~	c	45	31	54
	<i>Glechoma hederacea</i>	6	csr	36	43	17
	<i>Poa trivialis</i>	7	csr	45	31	43
	<i>Ranunculus repens</i>	7 ~	csr	17	11	25
	<i>Rubus caesius</i>	x	c	43	46	3
	<i>Urtica dioica</i>	6	c	74	81	22

In the bank habitats, 17 of the species we found were recorded in the Red List of Germany. In grassland, we recorded a total of 23 Red List species ($\approx 10\%$ of the total species) and in the copse relevés we found 10 Red List species.

Most Red List species were floodplain species adapted to moist site conditions, flooding or alternating water levels (e.g. *Carex vesicaria*, *Cnidium dubium*; tab. 2-3). In contrast to the most frequent species (tab. 2-2), which were dominated by competitors (c-strategists), only 20% of the Red List species were competitors (tab. 2-3), 80% showed a stress, ruderal or intermediate strategy. 25% of the total Red List species were species of dry grasslands (indicated by an EVI for moisture of 3 and below). The most common Red List species were *Thalictrum flavum* in the bank relevés (8%), *Ulmus minor* in the copse relevés (4%) and *Salvia pratensis* in the grassland relevés (13%).

Table 2-3: Red List species, frequencies in the respective habitats, and Ellenberg moisture value and strategy type. Species are attributed to one habitat type if their frequency in this habitat is at least 1% higher than in any of the other habitat types. All species with less than 1% difference in frequency are listed as 'equally frequent'. EM = Ellenberg moisture value (Ellenberg et al., 1991); ~ indicates adaptation to alternating water levels; = indicates adaptation to regular flooding; CSR = ecological strategy types according to Grime (1979); C = competitor, S = stress strategist, R = ruderal strategist; RL = Red List status according to Ludwig & Schnittler (1996); V = early warning list (vulnerable); G = endangerment of unknown magnitude; 3 = endangerment; 2 = strong endangerment.

	Species	EM	CSR	RL	Appears in % of records		
					Bank	Copse	Grassland
Bank	<i>Achillea ptarmica</i>	8	cs	V	2.59	0.88	
	<i>Cnidium dubium</i>	8 ~	c	2	3.45		1.04
	<i>Leonurus cardiaca</i>	5	c	3	0.86		
	<i>Pulicaria vulgaris</i>	8 =	sr	3	1.72		
	<i>Scolochloa festucacea</i>	10	cs	G	0.86		
	<i>Senecio paludosus</i>	9 =	cs	3	2.59		
	<i>Sonchus palustris</i>	8 ~	cs	V	1.72		
	<i>Stellaria palustris</i>	9 ~	csr	3	1.72		
	<i>Thalictrum flavum</i>	8 ~	c	V	7.76	0.88	
Copse	<i>Carex vesicaria</i>	9 =	cs	V		0.88	
	<i>Galeopsis segetum</i>	4	r	V		1.75	
	<i>Populus nigra</i>	8 =	c	3	1.72	3.51	
	<i>Ulmus minor</i>	x ~	c	3		4.39	

Table 2-3 (continued)

Grassland	<i>Allium angulosum</i>	8 ~	csr	3			2.08
	<i>Aquilegia vulgaris</i>	4	c	V			1.04
	<i>Briza media</i>	x	s	V			1.04
	<i>Carex praecox</i>	3 ~	csr	3	0.86		2.08
	<i>Centaureum pulchellum</i>	x ~	sr	V			1.04
	<i>Dianthus carthusianorum</i>	3	csr	V			3.13
	<i>Dianthus deltoides</i>	3	csr	V			3.13
	<i>Eryngium campestre</i>	3	cs	V	1.72		4.17
	<i>Helichrysum arenarium</i>	2	csr	3			1.04
	<i>Luzula campestris</i>	4	csr	V			1.04
	<i>Primula veris</i>	4	csr	V			5.21
	<i>Rhinanthus minor</i>	4	csr	V			4.17
	<i>Salvia pratensis</i>	3	csr	V	0.86		12.5
	<i>Sanguisorba officinalis</i>	6 ~	c	V			7.29
	<i>Silaum silaus</i>	x ~	c	V	0.86		3.13
	<i>Tragopogon pratensis</i> s. <i>orientalis</i>	5	csr	V			1.04
	<i>Trifolium montanum</i>	3 ~	csr	V			3.13
	<i>Trifolium striatum</i>	3	sr	3			1.04
	<i>Veronica verna</i>	2	sr	V			3.13
equally frequent	<i>Butomus umbellatus</i>	10 ~	cs	V	0.86	0.88	
	<i>Corrigiola litoralis</i>	7	r	3		0.88	1.04
	<i>Phleum phleoides</i>	3	csr	V	0.86		1.04
	<i>Thelypteris palustris</i>	8	cs	3	2.59	1.75	
	<i>Viola tricolor</i>	?	r	V		0.88	3.13

In the NMS, vegetation relevés for all habitats could be distinguished mainly by their geographic distribution, i.e. their location in plains or mountainous areas (a priori selected groups 1, 3 and 4 vs. groups 2 and 5). This was also indicated by the y (and x for the copse dataset) coordinates, which correlated to axis 1 for all three datasets (fig. 2-2 a – c). Here, some of the Elbe relevés (fig. 2-A1 in the appendix) were separated from the rest in the direction of the vectors related to x-coordinate, continentality and moisture value (fig. 2-2 c).

Study sites located in the plains of North-Eastern Germany (rivers Elbe, Oder and Havel, compare fig. 2-A1 in the appendix) with low intensity of bank regulation (either without bank protection or groynes) and low intensity of shipping traffic were related to a high Ellenberg moisture value, a high proportion of grassland in the surrounding landscape, a high light value (for bank and copse), and a high continentality value. Relevés located in

mountainous areas in (South-) Western Germany were related to higher biodiversity indices, higher Ellenberg values for soil acidity and temperature for the bank relevés and higher light values for grassland.

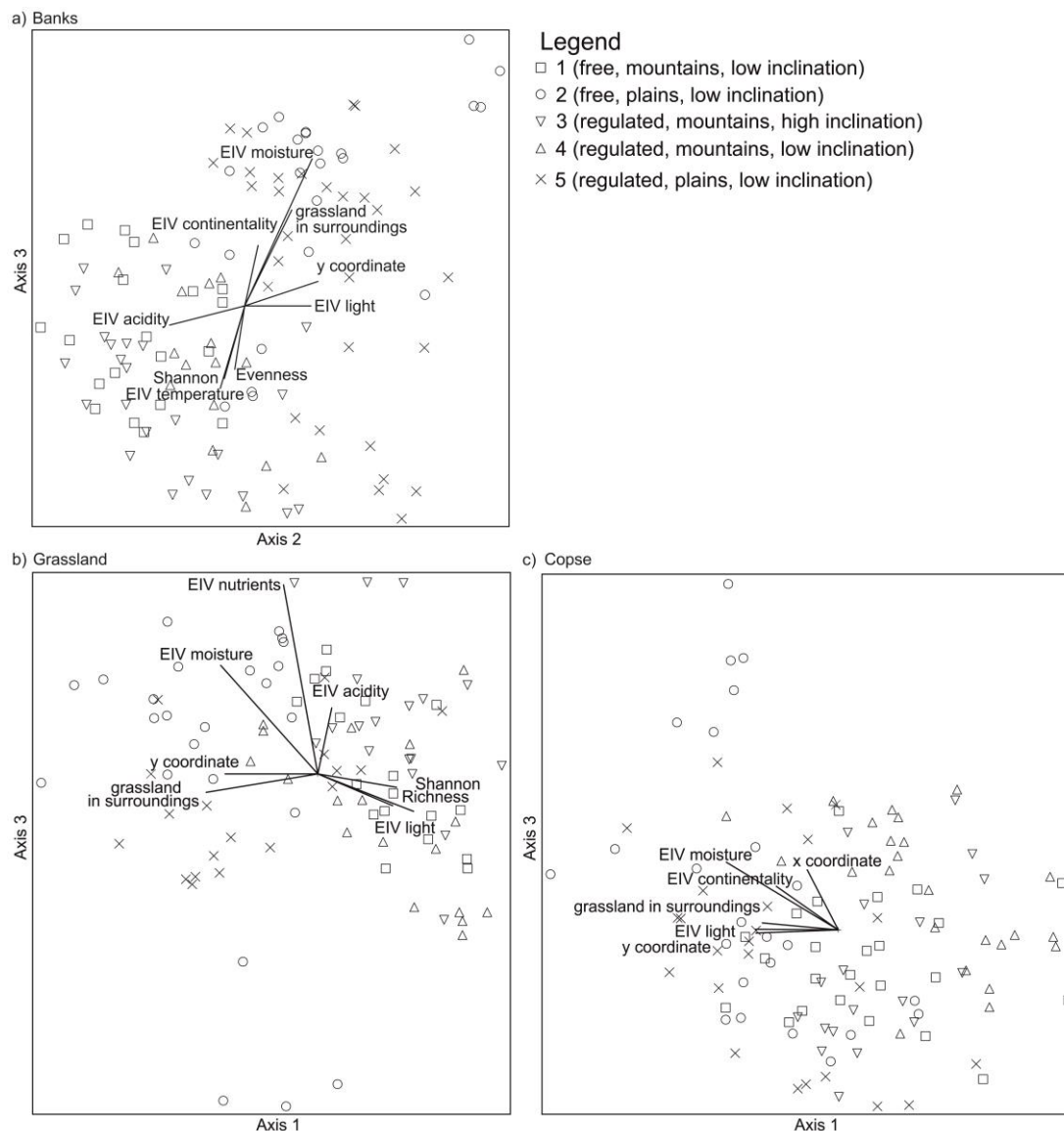


Figure 2-2: Final NMS plot for the respective datasets. Every point refers to one relevé, grouped by the a priori defined classes 1- 5 (see tab.2-1). In the analyses for all three datasets, the plots are mainly separated along axis 3. Environmental variables that correlate with either axis with $R^2 > 0.25$ are indicated in the figures, axes are unrotated, axes with highest R^2 are displayed (see fig. 2-A1 for further details). Refer to tab. 2-A1 for a detailed description of the environmental variables. A) Bank data, axis 2 vs. axis 3 (final NMS with three axes; final stress = 20.12; axis 1 not shown). B) Grassland data, axis 1 vs. axis 3 (final NMS with three axes, final stress = 20.17; axis 2 not shown). C) Copse data, axis 1 vs. axis 3 (final NMS with three axes, final stress = 22.63; axis 2 not shown).

46 environmental variables were included in the forward selection in CCA. Since the proportions of settlement in the landscape (within the study sites and within 1 km outside the sites) were linearly dependent on the other land-use classes, they were ignored in the calculations. The detailed results of CCA are displayed in tab. 2-4.

For the bank dataset, all environmental variables proved significant in forward selection. They accounted for 38.1% of the total variance in plant species composition when controlled for spatial autocorrelation. Forward selection for the grassland data resulted in 39 significant variables, which explained 33.4% of the total variation in the floristic composition (controlled for spatial autocorrelation). In the copse dataset, 40 of the 46 environmental variables were significant in forward selection. They accounted for 32.8% of the total variation in plant species composition.

Regional specifics like topography and climate, the EIVs, ground cover, and landscape (land use and landscape structure) had significant net effects in all habitat types. EIVs, which are a predictor for local site conditions, had the highest net effect in all habitats, followed by landscape structure and land use intensity. River management explained a small, but significant proportion of the variance for bank and grassland, but was not significant at 5% level for copse.

Table 2-4: Partial CCA for bank, grassland, and copse. The effects of the explanatory variable groups (Expl. variable) were quantified, controlling for spatial autocorrelation (SP). Variable groups are explained in detail in tab. 2-A1. Only significant variables are shown ($p\text{-value} \leq 0.05$). Covar. = covariables, Eigenv. = sum of canonical eigenvalues (total inertia bank = 7.07, total inertia grassland = 5.46, total inertia copse = 6.66), Expl. = explained, F = F -ratio for the test of significance for all canonical axes (test on the trace), P = corresponding p -value.

Expl. variable	Covar.	Eigenv.	Expl. Variation (%)	Expl. Variance (%)	F	P
Bank						
All variables, SP		3.2	45.07	100	2.8	0.001
All variables	SP	2.7	38.09	84.5	2.3	0.001
SP	All variables	0.1	0.74	1.6	1.3	0.078
Net effects						
topography	SP, All variables	0.2	2.57	5.7	1.2	0.015
climate	SP, All variables	0.1	1.47	3.3	1.4	0.031
ground cover	SP, All variables	0.2	2.94	6.5	1.4	0.002
river mgmt	SP, All variables	0.1	1.48	3.3	1.4	0.006
landscape	SP, All variables	0.2	3.26	7.2	1.5	0.001
EIV	SP, All variables	0.4	5.90	13.1	1.8	0.001

Table 2-4 (continued)

Gross effects						
topography	SP	0.5	7.61	16.9	2.2	0.001
climate	SP	0.4	5.94	13.2	2.8	0.001
ground cover	SP	0.4	5.96	13.2	2.1	0.001
River	SP	0.3	3.72	8.3	2.6	0.001
river mgmt	SP	0.6	8.53	18.9	3.1	0.001
landscape	SP	1.2	16.88	37.5	2.9	0.001
EIV	SP	0.9	12.14	26.9	3	0.001
Soil	SP	0.5	0.00	0.0	3.1	0.001
Grassland						
All variables, SP		2.5	45.99	100	3.6	0.001
All variables	SP	1.8	33.37	72.6	2.6	0.001
SP	All variables	0.0	0.60	1.3	1	0.521
Net effects						
climate	SP,All variables	0.1	1.70	3.7	1.4	0.039
river mgmt	SP,All variables	0.1	1.87	4.1	1.5	0.012
landscape	SP,All variables	0.1	2.34	5.1	1.3	0.041
EIV	SP,All variables	0.4	7.98	17.4	2.7	0.001

Table 2-4 (continued)

Gross effects						
topography	SP	0.3	5.07	11.0	3.1	0.001
climate	SP	0.4	6.52	14.2	2.7	0.001
vegetation	SP	0.1	2.02	4.4	2.4	0.001
River	SP	0.2	3.57	7.8	2.1	0.001
River mgmt	SP	0.4	7.8	17.0	2.4	0.001
landuse	SP	0.9	16.3	35.5	3.2	0.001
EIV	SP	0.7	13.3	29.0	3.6	0.001
Soil	SP	0.4	6.8	14.8	2.8	0.001
Copse						
All variables,		2.7	40.62	100	2.8	0.001
SP						
All variables	SP	2.2	32.75	80.6	2.1	0.001
SP	All variables	0.1	1.68	4.1	1.4	0.009
Net effects						
	SP,All					
topography	variables	0.1	1.55	3.8	1.3	0.009
	SP,All					
landscape	variables	0.3	4.41	10.9	1.5	0.001
	SP,All					
EIV	variables	0.5	6.77	16.7	2	0.001
Gross effects						
topography	SP	0.2	2.71	6.7	1.8	0.001
climate	SP	0.3	4.12	10.1	1.9	0.001
River	SP	0.2	2.80	6.9	1.9	0.001
river mgmt	SP	0.5	7.52	18.5	2.7	0.001
landscape	SP	1.0	14.61	36.0	2.8	0.001
EIV	SP	0.7	11.23	27.7	2.8	0.001
Soil	SP	0.4	0.00	0.0	2.5	0.001

2.3.2 Biodiversity distribution

Along the banks, we found 309 plant species (116 relevés), which represented about 9% of the German flora (3319 species, Korneck *et al.*, 1998). These habitats had a mean of 18 species per relevé (± 0.7 SE) and 49 species per site (± 4.4 SE). The mean Shannon index was 2.1 (± 0.06 SE) and mean evenness was 0.74 (± 0.02 SE). In the 96 grassland relevés, we recorded a total of 220 vascular plant species (7% of the German flora), with a mean number of 15 species per relevé (± 0.70 SE) and 40 species per study site (± 3.52 SE). The mean Shannon index was 2.0 (± 0.07 SE), the mean evenness was 0.74 (± 0.02 SE). For the 114 copse relevés, 258 species were found (8% of the German flora). The mean number of species per relevé was 17 (± 0.58 SE) and the mean number per site was 53. (± 3.56 SE). The mean Shannon index was 2.0 (± 0.04 SE). Evenness had a mean of 0.74 (± 0.01 SE).

Table 2-5: Summarized results of the univariate GRMs. Only those environmental variables (cf. tab. 2-A1) are listed that were included in forward selection and that have an EV of 10% or higher. The complete results including those of the multivariate GRMs are shown in tab. 2-A2 in the appendix. P = p -value, β^* = direction of relation (positive or negative) of the standardized regression coefficient, $EV\%$ = explained variance.

	Univariate GRM's								
	Species richness			Shannon			Evenness		
	β^*	P	EV%	β^*	P	EV%	β^*	P	EV%
Bank n = 116									
Intercept		≤ 0.001			≤ 0.001			≤ 0.001	
YX (spatial component)	-	≤ 0.001	11.6						
Geogr region	-/+	≤ 0.001	20.5						
Remaining floodplain	-	≤ 0.001	15.6						
Waterway class				-	≤ 0.001	30.2			
Soil type				-	≤ 0.001	15.6			
Soil landscape							-/+	≤ 0.001	30.5
Error			29.5			29.4			42.2
Grassland n = 96									
Intercept		≤ 0.001			≤ 0.001			≤ 0.001	
EIV light	-	≤ 0.001	8.9	-	≤ 0.001	11.8	-	0.011	4
EIV nutrients	-	≤ 0.001	15.6	-	≤ 0.001	17			
Bank protection	+	0.001	7.2	-	≤ 0.001	11.8	-/+	≤ 0.001	37.7
Soil landscape	-	≤ 0.001	31.2						
Error			31.4			42.5			53.2

Table 2-5 (continued)

Copse									
n = 114									
Intercept				0.017			≤ 0.001		
Bank protection	-/+	0.001	7.6	-/+	≤ 0.001	20.2	-	0.001	12.4
EIV light	+	≤ 0.001	10.3	+	≤ 0.001	6.8			
Proportion of settlement	-	≤ 0.001	6.6	-	≤ 0.001	15			
Landscape diversity							-	≤ 0.001	10.1
soil landscape	-/+	≤ 0.001	10.7						
Error			37.7			51.9			70.7

Similar to the results for species distribution, multivariate GRM identified regional differences (variables related to geographic location, topography, soil and climate), local site conditions (EIVs, ground cover) and landscape specifics (land use intensity and landscape structure), as well as variables related to the river and river management (e.g. waterway class), distance to the river channel, bank protection) as the main factors related to biodiversity. These patterns were valid for all habitat types, while the strength of influence differed (see Wilks Lambda values, tab. 2-A2 in the appendix).

In the univariate models, the correlations with the biodiversity indices species richness, Shannon diversity, and evenness differed in their significance between habitats.

For the *bank* relevés, the univariate models for richness and Shannon diversity had the highest explanatory power (both 70% EV, $R^2 = 0.701$ and 0.822 , respectively, see tab. 2-A2 in the appendix), while the model for evenness had 58% EV ($R^2 = 0.738$). Topographic, regional and soil related parameters had a strong influence (20 – 30% EV) in most univariate models. For local site conditions, only the Ellenberg temperature value showed a marginal positive relation to evenness (tab. 2-A2 in the appendix). Land use did not contribute to the explained variance of richness or Shannon and only marginally to that of evenness (tab. 2-A2 in the appendix). Factors related to river management were related to diversity in different directions: Bank protection by groynes and pavement had a marginal positive effect on Shannon index, waterway class was negatively related (tab. 2-5).

Regulation had a marginal negative effect on richness. The proportion of the functional floodplain ('remaining floodplain' as an inverse proxy for relative floodplain loss) was negatively related to richness.

For *grassland*, the univariate GRM for richness had the highest explanatory power (69% EV, $R^2 = 0.698$), followed by Shannon (57% EV, $R^2 = 0.620$). For evenness, it dropped to 47% EV ($R^2 = 0.435$). In contrast to the bank data, only one variable related to geographic differences (soil landscape) was significant, but it had the highest explanatory power of all significant variables for richness (31% EV). Here, the EIVs for nitrogen and light were negatively related to all biodiversity measures. Bank protection strongly correlated with evenness in the grassland relevés (38% EV), and also contributed significantly to Shannon diversity values and richness. Areas without bank protection or with groynes were related negatively to evenness and Shannon diversity, while bank protection by rocks (rip rap) had a significant positive relation with richness and evenness (tab. 2-A2 in the appendix).

The total variance explained in the univariate GRMs for *copse* was lower than for the other two datasets and dropped from 62% for richness ($R^2 = 0.597$) to 48% for Shannon ($R^2 = 0.406$) and 29% for evenness ($R^2 = 0.323$). Bank protection was the factor with the highest explanatory power for Shannon and evenness; it also contributed to the variance explained for richness. Similar to the other datasets, natural banks and groynes were negatively related, rip rap and pavement were positively related to biodiversity (tab. 2-A2 in the appendix). Similar to grassland, only the soil landscape as a geographic factor was correlated to richness. For landscape-related variables, the proportion of settlement within the study sites corresponded negatively to Shannon diversity and richness, and landscape structure diversity negatively influenced evenness (tab. 2-5). In contrast to grassland, the EIV for light was positively related to richness and Shannon diversity in copse stands.

2.4 Discussion

2.4.1 Species composition and ecological value

Plant species composition in the studied banks habitats reflected a gradient of anthropogenic intervention. The banks were mainly vegetated by biennial and perennial herbs that have a demand for high moisture and nutrient levels. In areas with impoundments and therefore limited disturbance events, plant species adapted to shallow water zones with low flow velocity dominate (Ellenberg, 2009), e.g. *Phragmites australis* (which occurred in 27% of our relevés). In areas with stronger currents (either rivers

without impoundments like in classes 1 and 2, tab.2-1, or channelized rivers with increased flow velocity), *Phalaris arundinacea* (with a frequency of 52% in our study) dominates the bank vegetation (Ellenberg, 2009).

The vegetation of the copse stands included species with a wide range of habitat preferences (Ellenberg, 2009). *Salix alba*, a species adapted to high flooding frequencies, occurred in 40% of the relevés. The occurrence of *Acer pseudoplatanus* (in 25% of the relevés) or *Fraxinus excelsior* (in 29% of the relevés) indicates less frequent flooding. Mosner *et al.* (2015) showed that especially these ‘hardwood species’ react strongly to changes in flooding regime. It is worth noting that this pattern occurred despite all copse relevés being located within a 500 m distance from the river bank and within the functional floodplain. However, in NMS and CCA, distance from river was not significantly related to species distribution. This might on the one hand be related to topographic specifics of the study sites (e.g. lower elevations at the outer border of the floodplain). On the other hand this might suggest that altered river dynamics and a reduction in flooding – often caused by deepening of the river bed due to anthropogenic alterations (Malanson, 1993) - facilitated the spread of flood-intolerant species (e.g. *Acer pseudoplatanus*) close to the river. Thus the schema of floodplain vegetation zonation as described e.g. by Ellenberg (2009) seems not to be valid any more since the vegetation of upper and lower terraces intermingle. This pattern is similar to the findings of Van Looy *et al.* (2004) in floodplain forest fragments along the river Meuse in Belgium. In their study, flooding frequency best explained species distribution, while distance to river channel had less explanatory power. Grassland was mainly composed of widespread meadow species, which are typical for mesophilic grasslands (*Arrhenatherum elatius*, *Dactylis glomerata*, *Achillea millefolium*; Ellenberg, 2009). Dryness indicators, some of which are also indicated in the Red List (tab. 2-3), occurred only in a small number of relevés. Even though moisture indicators were fairly frequent, only few species (e.g. *Allium angulosum*, *Cnidium dubium*, *Carex praecox*, *Silaum silaus*) belonging to the highly endangered (European Habitats Directive, The Council of the European Communities, 1992) *Cnidion* or *Molinion* were found. It is well established that these species are lost on sites with high soil phosphate levels and thus are conserved mainly in the areas behind the (lower) summer dikes which are less frequently flooded by river water with high phosphate loads (Elbe: Härdtle *et al.*, 2006; Rhine: Klaus *et al.*, 2011). In accordance to their findings that under high nutrient inputs *Cnidion* meadows are replaced by *Elymus* grasslands, *Elymus repens* occurred in 54% of

the sampled grassland relevés in the present study. This trend is further supported by the finding that high Ellenberg nutrient values were negatively correlated to biodiversity.

In general, the degradation of potential floodplain habitats was mainly visible in grassland vegetation, and to a lesser degree in the vegetation of bank and copse sites. However, it is important to note that all sampled copse patches were rather small, and one quarter of them contained *Acer pseudoplatanus*. This is a species of the zonal woody vegetation of Europe but can invade riparian forests if the abiotic conditions are suitable (less frequent flooding, Carbiener & Schnitzler, 1990). Extensive alluvial forests were absent from most study sites, thus the sampled stands were either relicts of former floodplain forests or they were planted.

2.4.2 Driving factors for species composition and biodiversity

According to Malanson (1993), the diverse effects of river alteration are variable due to geographic differences related to climate, soil, topography and the characteristics of the river basin. Similarly, we found that species distribution and diversity were mainly related to geographic factors and local site conditions (tab. 2-4 and 2-5). The high explanatory power of the EVIs in our analyses might in part be a consequence of the fact that these are derived directly from the species themselves; and because they represented a relatively large group in the CCA, their explanatory power was increased. On the other hand, they reflect local site conditions and have widely been used and acknowledged as surrogates for on-site measurements of environmental factors, where these are not feasible (Diekmann, 2003).

In NMS, relevés were mainly split according to their geographic location (fig. 2-2). Areas in the mountainous regions of Germany differed from the north (-eastern) lowland locations due to increasing continentality and differences between upstream and downstream structure of the rivers (Ward *et al.*, 2002). Accordingly, Ludewig *et al.* (2014) detected changes in vegetation patterns of wet meadows along the regional climatic gradient at the Middle Elbe River. Holmes *et al.* (2005) showed that species distribution is closely connected to the dominating intrinsic environmental gradients and their complex interactions in landscapes, and that flooding is the most important driver.

In our study the correlation between human alterations and species composition and biodiversity remained visible despite the confounding geographic and local differences. Also in studies by Martins *et al.* (2013) and Tabacchi *et al.* (1996) species abundance and

distribution was not only related to natural, but also to human impacts. In accordance, our results showed that land use and landscape structure (cf. Méndez-Toribio *et al.*, 2014) and to a lesser degree river management (cf. Catford *et al.*, 2011) were drivers of species composition and diversity in the floodplain habitats under study.

Catford *et al.* (2011) report a shift in species composition from typical floodplain species to more common, less specialized species along regulated rivers. Also a trend, a shift towards more terrestrial species has been frequently shown when rivers were regulated or channelized (cf. Poff & Zimmerman, 2010). Main drivers of this ‘terrestrialization’ in floodplain ecosystems are alterations of the flow regime, the flooding frequency and the deepening of the river bed (Allan, 2004, Deiller *et al.*, 2001, Poff & Zimmerman, 2010, Catford *et al.*, 2011). River embankments disrupt the connection between the river channel and the floodplain and thus have similar effects (Décamps *et al.*, 1988). Our results are in accordance with those patterns, especially in the bank and grassland habitats. In areas with artificial embankments (rip rap or pavement), diversity and evenness were increased since more terrestrial species can occupy these habitats, which were restricted to specialized species before regulation. We found similar results along a canal (Harvolk *et al.*, 2014). However, the results of other studies about the relation of floodplain biodiversity and construction of the riparian system remain ambiguous. While Chipps *et al.* (2006) and Poff & Zimmermann (2010) show that anthropogenic alterations of flooding regimes decrease species diversity, Deiller *et al.* (2001) report an increase in diversity with reduction of flooding.

Similarly, in accordance to other studies we found that regulation by barrages was negatively related to species richness (Dynesius *et al.*, 2004; Jansson *et al.*, 2000). Also a high waterway class – which indicates a high amount of shipping traffic and a higher degree of construction - had a negative correlation with Shannon diversity. Likewise, Willby & Eaton (1996) report negative relations between emergent vegetation diversity and traffic in navigable canals. In accordance with our finding that the influence of human impact was stronger for biodiversity than for composition, Dynesius *et al.* (2004) found that plant species richness differed between altered and natural rivers but species composition remained comparable.

Apart from anthropogenic changes to the river morphology and flow regime, land use and landscape structure were significantly related to species composition in all habitats under investigation. Also Méndez-Toribio *et al.* (2014) and Allan (2004) related these influences to elevated nutrient levels in the landscape due to intensive land use, which was also

reflected in the influence of the Ellenberg nutrient value in our results. Similarly, McCollin *et al.* (2000) relate changes in plant communities to soil nitrogen; Klaus *et al.* (2011) show that the distribution of *Cnidion* meadows is strongly influenced by soil phosphorus (see chapter 4.1).

Interestingly, biodiversity of the grasslands was negatively related to a higher proportion of grassland in the area. While we assume that a high proportion of grassland in a landscape is an indicator for less intensive land use (in comparison to arable or urban areas), we might guess that large connected grassland areas are more intensively managed than smaller, scattered grassland patches and could thus explain lower species numbers within the grassland itself (e.g. Kleijn *et al.*, 2009). This is the case for example in study site 2 D (the site with the highest proportion of grassland with 58% of the area), which is located in the Lower Rhine Region, a region with intensive livestock and fodder production (Statistische Ämter des Bundes und der Länder, 2014). For the copse stands, intensive land use was negatively related to biodiversity. The riparian forest fragments have a species composition (in the herb and shrub layer) that was relatively comparable to natural floodplain forests, thus they were sensitive to the effects of intensive land use (e.g. changing hydrological regimes, fragmentation of the landscape, increased nutrient loads; Naiman & Turner, 2000). Landscape diversity was negatively related to species diversity. This is in accordance with Naiman & Turner (2000), who showed that increased landscape fragmentation reduced diversity in floodplains.

The high diversity of natural floodplain systems is mostly due to the complexity of dynamic habitats (Allan, 2004; Ernoult *et al.*, 2006, Mathar *et al.*, 2015), which is a consequence of frequent disturbance by flooding, while single floodplain habitats are not necessarily species-rich (e.g. *Phragmites* or *Phalaris* reeds, Moelder & Schneider, 2011). Habitats that provide space for a higher number of terrestrial species, e.g. when natural dynamics through flooding decrease, can thus sustain higher total species numbers (Deiller *et al.*, 2001). Our overall findings are in accordance with Baart *et al.* (2013). They found that in riparian habitats disconnected from the river, the number of habitats declines but species diversity per se does not change, since the remaining habitats, which are less adapted to riparian influence, contain higher species numbers and experience shifts from pioneer to common species. This trend was also reflected in our findings that ruderal and stress strategists are replaced by competitors.

This highlights the notion that merely species diversity is not a reliable measure of ecosystem quality but that composition also needs to be considered (Deiller *et al.*, 2001;

Harvolk *et al.*, 2014). This in mind, even a decline of species diversity subsequent to the restoration of a riparian system can indicate an increase in ecosystem quality (Deiller *et al.*, 2001). In a restoration project along the Danube in Austria similar conflicts arose (Funk *et al.*, 2013). There, artificial bank habitats with low flow velocities supported high species diversity but would be destroyed if the floodplain was reconnected to the river. Still, this might have been desirable since more natural alluvial habitat types that sustain typical and protected species groups would arise (Funk *et al.*, 2013).

2.4.3 Recommendations for the management of heavily modified rivers

If river management, such as the maintenance of German Federal Waterways, should incorporate the demands of nature conservation and the protection of biodiversity, the potential conflict between increasing species numbers and increasing naturalness needs to be considered. A more natural riparian system is not necessarily a system with higher species numbers, at least in the short term (Baart *et al.*, 2013). An increase in species and habitat diversity could be achieved by an alteration of the flooding regime to a more diverse and/or natural state (Naiman & Turner, 2000). Also Mathar *et al.* (2015) identified a dynamic flood regime as one of the most important factors for adequate diversity in floodplain meadows.

Thus, our results suggest that increasing river-floodplain connectivity, e.g. by removal of bank protection or by establishment of more natural flow regimes in regulated rivers (Alfredsen *et al.*, 2012), might greatly improve the ecological status of floodplains along intensely managed rivers. Nature conservation needs to work within the given economic boundaries, but on the other hand, the ability of economy to work within the limitations of nature conservation also plays a key role when managing the interests in systems under anthropogenic pressure (Gibbs *et al.*, 2007), such as Federal Waterways.

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Appendix

Table 2-A1: Detailed overview of explanatory variables, their grouping in CCA, their respective factor levels and references.

Group	in	partial		
CCA	Variable	Explanation		Reference
Spatial Component	X			Recorded
	Y			Recorded
	Y2	cubic trend-surface polynomial (Borcard <i>et al.</i> 1992)		Calculated
	X2			Calculated
	YX			Calculated
	Y3			Calculated
	X3			Calculated
	X2Y			Calculated
	XY2			Calculated
Topography	Geogr region	main geographic and soil regions		BGR, 2013
		1	coastal region	
		2	broad river valleys	
		3	hilly lowlands	
		4	mountainous areas and Central German uplands	
	Elevation	elevation, measured with GPS and verified with Digital Elevation Model		DEM 10
	Slope			DEM 10
	Eastness	sin(aspect)		DEM 10
	Northness	cos(aspect)		DEM 10

Climate	Precipitation	mean annual precipitation	DWD, 2013
	Temperature	mean annual temperature in 1/10 degrees Celsius	DWD, 2013
	Climate zone	climate zone	BGR, 2013
		33 <i>temperate-suboceanic</i>	
		34 <i>temperate-suboceanic to temperate-subcontinental, partly mountainous</i>	
		35 <i>temperate-subcontinental</i>	
Coverage	Tree cover	percentage of cover of tree layer	Recorded
	Shrub cover	percentage of cover of shrub layer	Recorded
	Herb cover	percentage of cover of herb layer	Recorded
	Moss cover	percentage of cover of moss layer	Recorded
	Litter cover	percentage of cover of litter layer	Recorded
	Open water	percentage of cover of open water	Recorded
	Open soil	percentage of cover of open soil	Recorded
Vegetation	Height herb	Mean height of herb layer in meters	Recorded
	Height shrub	Mean height of shrub layer in meters	Recorded
	Height tree	Mean height of tree layer in meters	Recorded
River	Distance to		
	river	distance to river channel in meters	Recorded
	Flood 2013	sampling before or after flood in 2013	Recorded
River Management	Bank		Recorded
	protection	bank protection	
		1 <i>nature (no bank protection)</i>	

	2	<i>groynes</i>	
	3	<i>rock</i>	
	4	<i>pavement</i>	
	5	<i>wall</i>	
Waterway			BMVBS, 2009
class	Waterway class	(state of construction, size of ships that can use the waterway)	
	1	<i>III (ships with 67-70 m length, 8.2-9.0 m width and 470-700 t tonnage)</i>	BMVBS, 2009
	2	<i>IV (ships or pushing units with 80-85 m length, 9.5 m width and 1000-1500 t tonnage)</i>	
	3	<i>Va (ships or pushing units with 95-110 m length, 11.4 m width and 1500 - 3000 t tonnage)</i>	
	4	<i>Vb (pushing units with 172 - 185 m length, 11.4 m width and 3200 - 6000 t tonnage)</i>	
	5	<i>VIa (pushing units with 95-110 m length, 22.8 m width and 3200-6000 t tonnage)</i>	
	6	<i>VIb (ships with 140 m length and 15 m width or pushing units with 185-195 m length and 6400-12000 t tonnage)</i>	
	7	<i>VIc (pushing units with 285 m length and 22,8 m width or with 195-200 m length and 33-34.2 m width and 9600-18000 t tonnage)</i>	
Regulation	0	<i>Free-flowing</i>	BMVBS, 2009
	1	<i>Regulated by dams</i>	

	Remaining floodplain	proportion of the functional floodplain of the total (historical) floodplain	Brunotte <i>et al.</i> , 2009
Landscape	Proportion of arable land	proportion of arable land within study site	ATKIS
Characteristics	Proportion of grassland	proportion of grassland within study site	ATKIS
	Proportion of forest	proportion of forest within study site	ATKIS
	Proportion of settlement	proportion of settlement within study site	ATKIS
	Arable land in surroundings	proportion of arable land within 1 km buffer around study site	ATKIS
	Grassland in surroundings	proportion of grassland within 1 km buffer around study site	ATKIS
	Forest in surroundings	proportion of forest within 1 km buffer around study site	ATKIS
	Settlement in surroundings	proportion of settlement within 1 km buffer around study site	ATKIS
	Landscape diversity	Shannon's diversity of landscape structure	biotope map

Edge density		Edge Density	biotope map
Ellenberg	EIV light	mean indicator value for light	Ellenberg
Indicator Values	EIV		
	temperature	mean indicator value for temperature	Ellenberg
	EIV		
	continentality	mean indicator value for continentality	Ellenberg
	EIV moisture	mean indicator value for moisture	Ellenberg
	EIV acidity	mean indicator value for reaction	Ellenberg
	EIV nutrients	mean indicator value for nitrogen	Ellenberg
Soil Characteristics	Soil type	dominating soil type in the area	BGR, 2013
		1 sand	
		2 loam	
		3 clay	
		4 peat	
	Soil acidity	amount of limestone and calcareous substrate in the area	BGR, 2013
		0 acid	
		0.5 partly calcareous	
		1 calcareous	
	soil landscape		BGR, 2013
	Soil landscape	(Ad-hoc AG Boden, 2005)	

- 1 *floodplains and lower terraces, associated with moorland and drifting sand areas*
 - 2 *older river terraces*
 - 3 *lowlands and glacial valleys of the young moraine landscape*
 - 4 *loess areas*
 - 5 *loess landscape of mountainous areas*
 - 6 *high amount of calcareous rocks, alternating with loess and residual loess*
 - 7 *high amount of calcareous rocks, alternating with residual loess and other cover sediments*
 - 8 *high amount of sandy, silty and clay rocks, often alternating with loess*
 - 9 *high amount of sandy, silty and clay rocks*
 - 10 *high amount of clay and silty rocks*
 - 11 *high amount of silty or calcareous shale with alternating amounts of graywacke, limestone, sandstone and quartzite, partly mixed with residual loess*
-

Table 2-A2: GRM results. Effects on species richness, Shannon index and evenness of bank, grassland and copse by the influence of topography, climate, soil, vegetation and river specifics, land use and landscape structure, local site conditions (derived from Ellenberg indicator values), and waterway management. Only those environmental variables are listed that were included in forward selection. P = p -value, β = standardized regression coefficient, MS = mean squares, df = degrees of freedom, $EV\%$ = explained variance.

Bank	Multivariate		Univariate														
	GRM		GRM's														
	n = 116		Species richness					Shannon					Evenness				
Effect	Wilks Λ	P	β	MS	df	P	EV%	β	MS	df	P	EV%	β	MS	df	P	EV%
Intercept	0.853	0.002		57.02	1	≤ 0.001			45.18	1	0.000			6.37	1	≤ 0.001	
YX (spatial component)	1.000		-0.63	70.37	1	≤ 0.001	11.6										
Geogr region	1.000			41.45	3	≤ 0.001	20.5										
2																	
4			-0.35														
3			0.47														
Northness	0.876	0.007						0.10	3.11	1	0.041	1.4					
Precipitation	1.000		-0.47	55.87	1	≤ 0.001	9.2										
Climate zone	0.722	0.000							7.13	2	≤ 0.001	6.3					
34								0.49									
33																	

[illegible]

Richness	0	0.735	≤ 0.001 0.701				≤ 0.001 0.822				≤ 0.001 0.738			
Shannon	0	0.795												
Evenness	0	0.741												

Table 2-A2 “Grassland”

	Multivariate		Univariate															
Grassland	GRM		GRM's															
n = 96			Species richness					Shannon					Evenness					
Effect	Wilks Λ	P	β	MS	df	P	EV%	β	MS	df	P	EV%	β	MS	df	P	EV%	
Intercept	1.000			113.180	1	≤ 0.001			22.670	1	≤ 0.001			5.234	1	≤ 0.001		
Y	1.000							-0.254	9.213	1	0.001	5.6						
Elevation	0.741	0.000																
Climate zone	0.621	0.000																
EIV light	0.817	0.002	-0.434	31.589	1	≤ 0.001	8.9	-0.409	19.306	1	≤ 0.001	11.8	-	0.238	2.150	1	0.011	4.0
EIV temperature	0.875	0.019																
EIV continentality	0.765	0.000																

EIV acidity	1.000							0.266	9.060	1	0.001	5.5							
EIV nutrients	0.689	0.000	-0.566	55.073	1	≤ 0.001	15.6	-0.488	27.796	1	≤ 0.001	17.0							
Landscape																			
diversity	1.000		-0.438	14.051	1	0.002	4.0	-0.260	9.226	1	0.001	5.6							
Distance to																			
river	1.000												0.244	2.743	1	0.004	5.1		
Waterway																			
class	0.468	0.000																	
Bank																			
protection	1.000			8.494	3	0.001	7.2		6.438	3	≤ 0.001	11.8		6.797	3	≤ 0.001	37.7		
4																			
3			0.239											0.305					
1													-						
													0.297						
2													-						
								-0.180					0.348						
Regulation	1.000			6.129	1	0.039	1.7												
0			0.248																
Soil																			
landscape	0.367	0.000		13.764	8	≤ 0.001	31.2												
1			-0.794																
Error				1.387	80		31.4		0.799	87		42.5		0.319	90			53.2	

	p-value	R ²		p-value	R ²		p-value	R ²		p-value	R ²
Richness	0.000	0.714		≤ 0.001	0.698						
Shannon	0.000	0.678					≤ 0.001	0.620			
Evenness	0.000	0.638								≤ 0.001	0.435

Table 2-A2 “Copse”

Copse	Multivariate		Univariate														
	GRM		GRM's														
			Species richness					Shannon					Evenness				
n = 114	Wilks	P	β	MS	df	P	EV%	β	MS	df	P	EV%	β	MS	df	P	EV%
Effect	Λ																
Intercept									1.029	1	0.017			0.595	1	0.000	
Y	1.000							-0.191	0.709	1	0.047	2.0					
XY²	1.000												-0.191	0.093	1	0.042	2.8
Geogr region	0.558	0.000															
Tree cover	0.767	0.000											-0.207	0.135	1	0.015	4.0
Height tree	0.901	0.026															
Height shrub	0.898	0.022															
Height herb	0.803	0.000	-	8.870	1	0.000	8.7										

Soil type	2	0.563																	
	1	0.221																	
	5	-																	
	4	0.658																	
	1.000	2.804				1	0.010		2.7										
acidity	1	-																	
	0.614	0.000		0.644															
Error		0.406		95		37.7		0.175		106		51.9		0.022		107		70.7	
		p-value		R²		p-value		R²		p-value		R²		p-value		R²			
Richness		0.000		0.608		0.000		0.597		0.000		0.406		0.000		0.323			
Shannon		0.000		0.566															
Evenness		0.000		0.530															

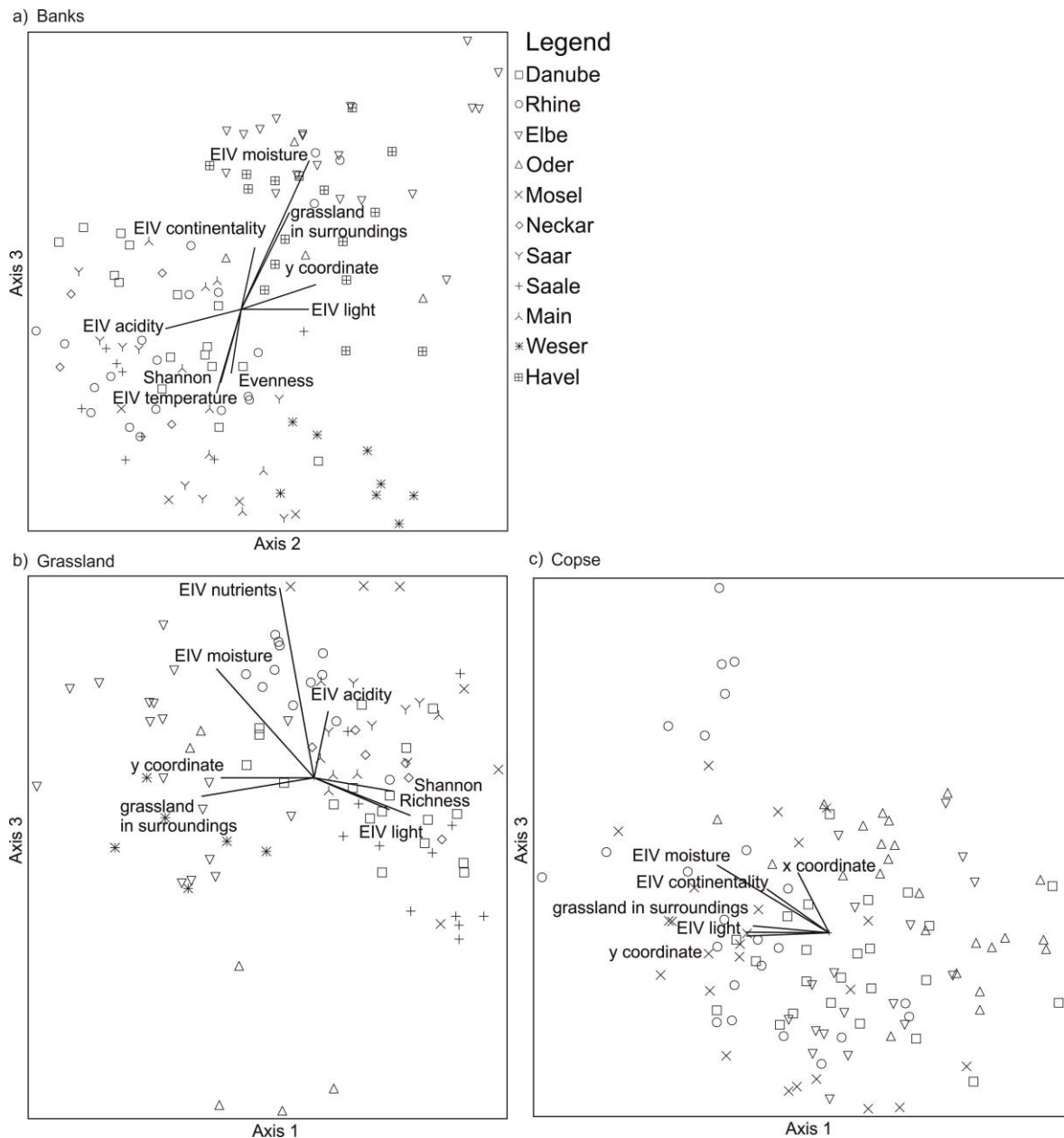


Figure 2-A1: Final NMS plot for the respective datasets, grouped by rivers.

A) Bank data, axis 2 vs. axis 3 (final NMS with three axes; final stress = 20.12; axis 1 not shown). The gain in R^2 is 0.108 for axis 1, 0.248 for axis 2 and 0.311 for axis 3. Environmental variables that are shown in the figure are y: $R^2 = 0.307$, moisture: $R^2 = 0.281$, light: $R^2 = 0.278$, acidity: $R^2 = 0.313$, all correlate with axis 2; proportion of grassland: $R^2 = 0.400$, temperature: $R^2 = 0.346$, continentality: $R^2 = 0.253$, moisture: $R^2 = 0.614$, Shannon: $R^2 = 0.303$, and Evenness: $R^2 = 0.264$, all correlate with axis 3.

B) Grassland data, axis 1 vs. axis 3 (final NMS with three axes, final stress = 20.17; axis 2 not shown). The gain in R^2 is 0.268 for axis 1, 0.134 for axis 2 and 0.285 for axis 3. Environmental variables that are shown in the figure are y: $R^2 = 0.354$, proportion of

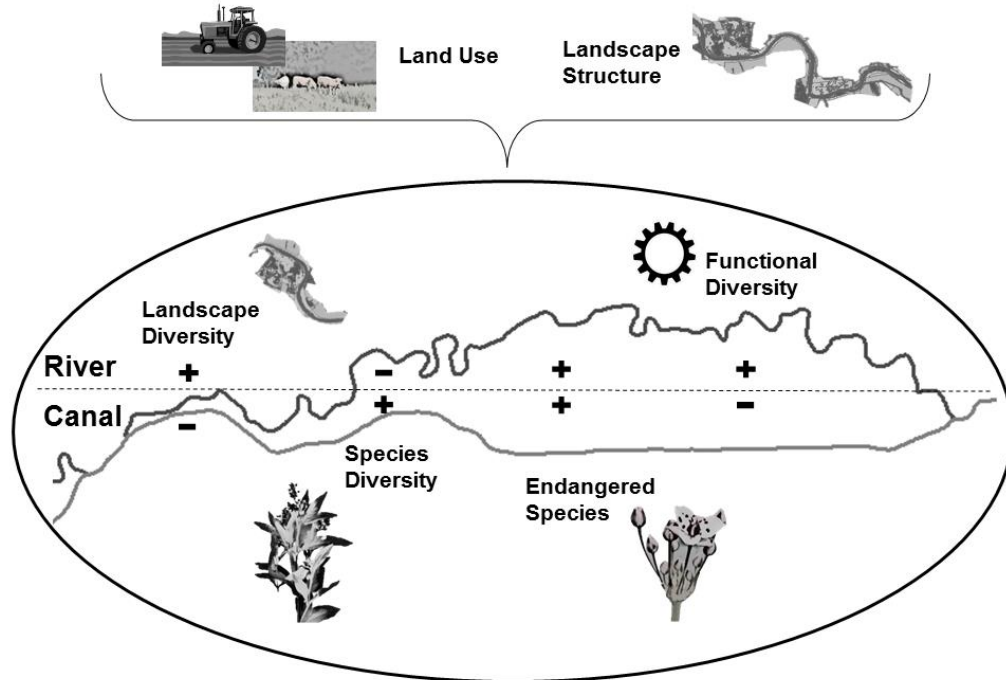
grassland: $R^2 = 0.425$, light: $R^2 = 0.285$, moisture: $R^2 = 0.370$, Richness: $R^2 = 0.366$, Shannon: $R^2 = 0.301$, all correlate with axis 1; moisture: $R^2 = 0.415$, acidity: $R^2 = 0.251$, and nutrients: $R^2 = 0.722$, all correlate with axis 3. C) Copse data, axis 1 vs. axis 3 (final NMS with three axes, final stress = 22.63; axis 2 not shown). The gain in R^2 is 0.214 for axis 1, 0.160 for axis 2 and 0.229 for axis 3. Environmental variables that are shown in the figure are x: $R^2 = 0.231$, y: $R^2 = 0.315$, proportion of grassland: $R^2 = 0.292$, light: $R^2 = 0.317$, moisture: $R^2 = 0.427$, continentality: $R^2 = 0.236$, all correlated to axis 1; and moisture: $R^2 = 0.258$, correlated to axis 3.

Chapter 3

Can artificial waterways provide a refuge for floodplain biodiversity?

A case study from North Western Germany

Sarah Harvolk, Lars Symmank, Andreas Sundermeier, Annette Otte and Tobias W. Donath



Abstract

Rivers and floodplains are among the most species-rich ecosystems in Middle Europe. Intensive anthropogenic influence has led to a loss of floodplain area and threatens their ecological functionality. This is especially the case for waterways, which have been subject to river engineering due to their economic importance and thus have lost a significant amount of their original floodplains and biodiversity. Canals as artificial waterways have been in the focus of reconciliation ecology, and they have been proven to serve as a refuge for several aquatic species groups where their original habitat is impaired or lost. However, the potential to preserve terrestrial macrophytes and biodiversity along their banks has rarely been considered. Thus the question arises whether canals can provide, at least partly, suitable habitat space to sustain species diversity and functionality of floodplains. In the present case study, we compared the floristic, functional and structural diversity of the floodplain and the respective adjacent areas of the river Ems and the Dortmund–Ems canal in North Western Germany, since both waterways run in parallel and are hydrologically connected. Species composition shows distinct differences between both waterways. Most species along the canal are mainly generalists adapted to anthropogenic influence, while species along the river are characteristic for floodplain systems. Species diversity is up to 10% higher along the canal due to higher lateral heterogeneity, while functional divergence and landscape structure diversity are up to 5% higher along the natural river. Diversity distribution patterns are mainly influenced by landscape structure and land use patterns. Numbers of endangered species did not differ significantly. Thus, the canal can serve as a habitat for single endangered floodplain species but it cannot substitute the functions of a natural dynamic floodplain. Increasing structural diversity and preserving the habitat function of the canal banks by an adapted management regime might enhance the ecological value of a heavily used artificial waterway within the given economic limitations.

3.1 Introduction

Rivers and floodplains are of high ecological value, yet they are highly endangered ecosystems (e.g., Palmer *et al.*, 2010; Stanford *et al.*, 1996; Ward, 1998). This is especially true for waterways, which are intensely managed and used for transportation (Wolter and Vilcinskas, 1997). By the end of the last century, 77% of the rivers in Europe, the Commonwealth of Independent States (CIS) and North America were seriously modified (Cowx and Welcomme, 1998). In Germany, modification and flood control measures led to a loss of two thirds of the original floodplain area (Brunotte *et al.*, 2009). Also the floodplains remaining are of low ecological value: only ten percent of them are in an ecologically functional state (Brunotte *et al.*, 2009).

This is alarming since riparian zones provide important ecosystem functions and services such as sediment transport and deposition, flood retention, groundwater re- and discharge, nutrient filtration and storage as well as carbon sequestration (Maltby *et al.*, 2009; Naiman and Decamps, 1997; Scholz *et al.*, 2012). They serve as ecological corridors for species dispersal and they provide habitat space, which results in exceptionally high levels of biodiversity (Naiman and Decamps, 1997). Vice versa, biodiversity is an important driver of ecosystem functionality (MEA, 2005; Naeem *et al.*, 1994) and therefore the functional biodiversity approach has received increasing attention during the last few years (Petchey and Gaston, 2006). Ecosystem functioning is rather driven by the traits and characteristics of species than by mere species numbers (Díaz and Cabido, 2001). In functional diversity research, the range and value of those traits (e.g., ability to fix nitrogen, growth form, dispersal mode) is studied and used as a measure of biodiversity. This approach has been widely acknowledged and is now integrated as a further essential aspect of biodiversity next to genetic, species and ecosystem diversity (Díaz and Cabido, 2001).

Biodiversity and functionality of riparian systems are strongly influenced by human activities, which change the river body itself, such as hydromorphological changes, river impoundment and water management (Naiman and Decamps, 1997). In addition, change and intensification of human land use influences riparian systems (Méndez-Toribio *et al.*, 2014). In concert, these activities caused the aforementioned loss in floodplain space and functionality. This has brought riparian systems to the attention of policy makers, starting with the Ramsar Convention on Wetlands (United Nations, 1971), the European Habitats Directive (92/43/EEC, The Council of the European Communities, 1992), the Convention on Biodiversity (CBD, United Nations, 1992) and the Millennium Ecosystem Assessment (MEA, 2005). The European Water Framework Directive (2000/60/EC, The European

Parliament, 2000) aims at a good ecological status of both natural and artificial water bodies like rivers and canals.

The resemblance between artificial water bodies and rivers is merely superficial (Annett 1998; Hatcher *et al.*, 1999). Canals have a regular structure, a negligible flow velocity, regulated water levels and therefore lack the dynamics of rivers (e.g., Hatcher *et al.*, 1999; Willby *et al.*, 2001). Due to those differences, they cannot provide the same functions like riparian systems in respect to e.g., nutrient cycling or flood retention. Still they provide habitat space, increase the connectivity within a landscape and thus might serve as migration corridors (Jesus Casas *et al.*, 2011). Canals are known to serve as secondary habitats for several fish (Waltham and Connolly, 2007; Wolter and Vilcinskis, 1997; Wolter, 2001), invertebrate (Grumiaux & Dhainaut-Courtois, 1996) and aquatic macrophyte species (Weber *et al.*, 2012; Willby and Eaton, 1996; Willby *et al.*, 2001) and rescue them from extinction when their natural habitat is impaired or lost, as described e.g., for *Margaritifera auricularia* in the Ebro River Basin by Gómez and Araujo (2008).

Even though the habitat function of canals seems to be well-studied, the existing literature mainly considers aquatic species. To our knowledge, studies concerning semiterrestrial and terrestrial macrophytes are scarce (Chester and Robson, 2013; but see Willby and Eaton, 1996; Goulder, 2008). It remains unclear if the banks and adjacent areas along a canal can provide secondary habitats for floodplain species and whether they can take over similar ecological functions as floodplains or if they form novel or emergent ecosystems, i.e., whose characteristics were changed through human impact and who, also after abandonment, will not return to their original state (Hobbs *et al.*, 2009; Milton, 2003). Consequently, Chester and Robson (2013) ask for more studies comparing artificial and surrounding natural water bodies with respect to biodiversity, assemblage composition and ecosystem function.

We followed their suggestion in the present case study. We compared the banks and floodplain of the German lowland river Ems and the banks and adjacent area of the Dortmund–Ems-canal (DEK). Both water bodies run in parallel within only a few kilometers' distance. They represent the extremes of a gradient of anthropogenic influence: the canal is artificially constructed and used for transportation whereas the Ems in the area concerned, has not been straightened and is not used for shipping traffic. We studied the bank vegetation and the surrounding biotope types along both water bodies using a paired design to analyze species composition and the ecological value of both systems. We calculated and compared measures for plant species diversity, functional diversity and

landscape diversity and we determined the main influencing factors on species diversity distribution to answer the following questions:

- To what extent do species composition, species diversity and functional diversity differ between both systems?
- Which landscape features are related to biodiversity patterns found along both waterways?
- Which conclusions can be drawn from our findings for biodiversity management along both systems?

3.2 Methods

3.2.1 Study area

The study area comprises the stretches of the Ems and the Dortmund–Ems canal (DEK, official German abbreviation) between the towns of Lingen and Meppen in North Western Germany (fig. 3-2a, between 52°28'039''N, 7°17'55''E and 52°39'58''N, 7°16'46''E). It is located in the northwest German lowlands in the physiogeographical region “Ems-Hunte-Geest and Dümmer Geest-Niederung” (Drachenfels, 2010). The soils in the area originate from valley sands and moraines, with local occurrences of fluvioglacial sands (BfG, 2006). The main soil types are gleys, podsoles and gley-podsoles (NIBIS, 2012). Climatically, the study area lies in the transition area between the oceanic and the continental zone, which results in a humid temperate climate with cool summers and warm winters (Lingen: mean annual temperature: 10°C; mean annual precipitation: 800 mm; DWD, 2013; BfG, 2008).



Figure 3-1: Photographs of the study areas, i.e. the structure of the canal (a), the banks of the canal with rip rap and tall perennials (b), the structure of the Ems (c) and the bank vegetation of the Ems (d).

The DEK was constructed in the 1890s to allow shipping traffic from the industrial area Ruhrgebiet to the North Sea. At the Gleese Lock near Lingen (2 km south of the study area), the DEK and the Ems unite. At the weir Hanekenfähr (southern end of the study area), the canal leaves the river and both water bodies run northwards in parallel until they unite again within the city area of Meppen (northern end of the study area). From Meppen to Papenburg, the river Ems is channelized and runs under the name of the Dortmund–Ems canal (WSA Meppen, 2013). The DEK is classified in European Waterway Class IV (WSV, 2013), with about 7000–9000 ships per year (WSA Meppen, 2013). The Ems is classified as non-shippable (European Waterway Class 0, WSV, 2013). According to the Water Framework Directive both water bodies are attested a poor ecological status or poor ecological potential (Geschäftsstelle Ems, 2010). The morphology of the DEK is similar to that of other artificial waterways (K.Geers, pers.comm.). The banks are structured uniformly with rip rap (fig. 3-1b) or sheet pile walls close to the sluices. Within short distance, it follows a grassland strip, which is occasionally vegetated with tall forbs or reeds at both banks. The banks on both sides of the canal are accompanied by a maintenance road, which separates them from the surrounding landscape. The structure of the canal is illustrated in fig. 3-1a. The adjacent areas are, except for the urban and industrial areas, mainly covered by forest (27%, vs. 16% arable and 9% grassland). In contrast, the Ems is a highly dynamic river in our study area with water level fluctuations of more than 3 m within one year (10 year annual mean at water gauge Dalum, NLWKN, 2013), while the water level fluctuations in the canal are limited to 4 cm between Hanekenfähr and Varloh and 20 cm between Varloh and Meppen, respectively (K.Geers, pers.comm.). Although some parts of the Ems banks (35%) are secured with rip rap to prevent erosion, these structures are much weaker than along the canal. Therefore, a high degree of dynamics is maintained; the sandy river banks are subjected to erosion. Apart from the eroded areas, the banks are vegetated with tall forbs and fragments of alluvial forests (fig. 3-1c and d). The surrounding area is mainly used as grassland (34%, vs. 32% arable land and 15% forest).

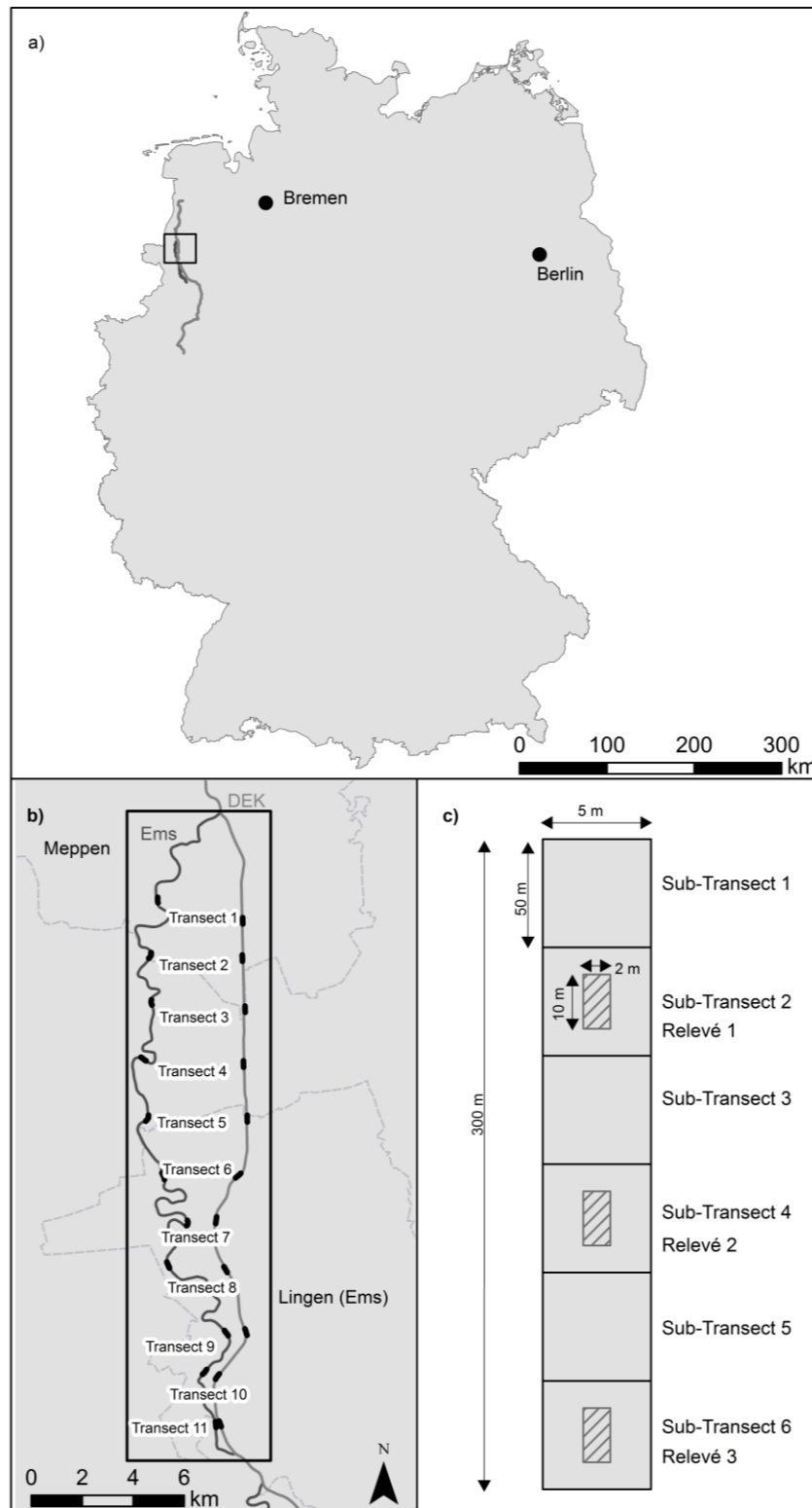


Figure 3-2: Location of the study area (a), location of transects for vegetation sampling (b), and sampling design (c). See text for a detailed description.

3.2.2 Data collection

Vegetation data

We sampled vegetation data in the transition zones between aquatic and terrestrial habitats along the river and the canal banks in summer 2013. Along each water body we established 11 transects of 300 m length and 5 m width (fig. 3-2c). The transects were divided into 50 m long sub-transects to account for spatial heterogeneity. Long and narrow plots of 100–500 m length are a standard design for recording riparian species richness patterns (Dynesius *et al.*, 2004) and are also effective for detecting rare species (Gentry, 1982). The transects were located with the main axis parallel to the water's edge, and were chosen pairwise for each river and canal location. The locations along each water body were approx. 2 km apart and alternating between the eastern and western bank (fig. 3-2b), to cover the total length of the area and the total range of natural conditions. Areas with non-typical conditions, like the direct surroundings of sluices, were excluded. We recorded presence/absence data for all vascular plant species in each sub-transect (referred to as 'P/A dataset'), as well as the mean height and coverage (%) of every vegetation layer, moss layer and open soil. In addition, we sampled cover for vascular plant species (referred to as 'abundance dataset') by placing relevés of 2 m 10 m in the center of every second 50 m sub-transect (fig. 3-2c). Species abundance was estimated using the modified Braun-Blanquet numerical scale, which approximates a square root transformation of cover percentages (Van der Maarel, 1979).

Landscape data

The biotope types in the area were mapped according to the biotope key of the BfG (2003) and ecologically evaluated on a 0–5 scale (0: no evaluation possible, 1: very low value, 5: very high value; BfG, 2006) in 2005 in the course of the development of a new management scheme. These datasets (ArcGIS shapefiles at a 1:2000 resolution) were used for analyses on the landscape scale. They include the water body and the surrounding areas, from 10 m to almost 900 m from the river/canal bank. The datasets were divided into stretches of 1 km length, 28 for the river and 29 for the canal. Information on land use in the study area was derived from a Digital Landscape Model 1:25,000 of the German Official Topographic Cartographic Information System (ATKIS-DLM 25, provided by the BfG).

3.2.3 Analyses

We applied non-metric multidimensional scaling (NMS) to detect differences in species composition between the river and the canal transects. We used the Sørensen distance measure (Bray–Curtis distance), two dimensions, starting configuration by random number and 50 iterations. Indicator species analysis was performed for the Ems and the DEK datasets (Dufrene and Legendre, 1997). All species with a significant ($p < 0.05$) indicator value (IV) higher than 25 were considered as indicator species. These analyses were done using PCOrd 5.32 (McCune and Mefford, 2006).

A paired t-test was employed to test for differences in Ellenberg indicator values, which are estimates for site conditions (Ellenberg *et al.*, 1991), measures of biodiversity (see below), number of Red List species, the area weighted means of valuable biotopes and the number of habitat types protected by the Habitats Directive (92/43/ EEC, The Council of the European Communities, 1992) per area (for each 1 km stretch extracted from the landscape dataset). T-tests were performed using Statistica 10 (Statsoft Inc., Tulsa, OK, USA).

Species diversity measures were calculated using the algorithms implemented in the software Turboveg (Hennekens and Schaminée, 2001), namely species richness, the Shannon–Weaver index (Shannon and Weaver, 1963), evenness (Hill, 1973), and the complementary Simpson’s index (1-D, Simpson, 1949).

To determine functional diversity, we used the functional richness, functional evenness and functional divergence measures (Villéger *et al.*, 2008) as well as functional dispersion (Laliberté and Legendre, 2010) and Rao’s quadratic entropy (Rao, 1982), using the package “FD” (Laliberté and Legendre, 2010) for the R statistical environment (R 2.14.2; R Core Team, 2014). These indices are applicable to describe the functional trait space for abundance as well as for presence absence data (Laliberté and Legendre, 2010). We used the traits guild, maximum height, life span, hemeroby, nautochory, tolerance for periodic wetness and flooding, and position of the regenerative organ since these are related to riparian influence and disturbance (tab. 3-A1). Trait values were derived from the databases LEDA (Kleyer *et al.*, 2008) and Biolflor (Klotz *et al.*, 2002), and from the Ellenberg indicator values (Ellenberg *et al.*, 1991).

We calculated the landscape structure diversity indices richness (number of classes), Shannon’s evenness (Shannon and Weaver, 1963), dominance (deviation from maximum diversity, Lang and Tiede, 2003) and Shannon’s diversity (Shannon and Weaver, 1963)

using the ArcGIS 10 (ESRI, Redlands, CA, USA) extension VLATE (Lang and Tiede, 2003), to gain insight on the diversity of biotopes along the river and the canal.

To identify explanatory variables for distribution patterns of biodiversity, we performed a regression tree analysis using the recursive partitioning method by Therneau and Atkinson (2013) as implemented in the R package “rpart” (Therneau *et al.*, 2013). The Shannon–Weaver index for every sub-transect served as a surrogate for diversity on species level and was used as a target variable for regression. Since we collected environmental data at the sub-transect level and since there were significant differences in diversity at species level (compare results section), it is reasonable to focus on this aspect of diversity in the regression analysis. We used only the P/A dataset since the higher number of sub-transects provided a higher number of cases for the analysis than the abundance dataset. We employed the same environmental variables for the recursive partitioning as those that served as the second matrix for the NMS (tab. 3-A2), namely information about topography (aspect), vegetation cover, the water body (Ems or DEK), land use, productivity, landscape structure and about adjacent biotopes.

3.3 Results

3.3.1 Vegetation data

Across the study areas, in total 253 plant species (presence/ absence; 163 in abundance dataset) were recorded, of which 125 (presence/absence; 69 in the abundance dataset) occurred in both studied systems. Of those species, in total 21 were listed in the Red List of Lower Saxony (Garve, 2004). Their occurrence, Ellenberg moisture value and strategy type (Grime, 1979) are summarized in tab. 3-A3. The number of Red List species per 300 m-transect along the DEK (3.2 ± 0.57 ; mean \pm SE) was not significantly different from the number of Red List species along the Ems (2.9 ± 0.71).

In the NMS the vegetation relevés were clearly grouped into a river and canal cluster (fig. 3-3). The canal cluster covered less ordination space compared to the river relevés since the plant species assemblages were less diverse among the relevés of the canal. The main environmental variables related to the axes were the proportion of grassland in the vicinity and the ecological value of the adjacent plots, which increased in the direction of the Ems cluster, and the edge density in the surrounding landscape and the proportion of forest in the area, which increased in the direction of the DEK cluster (fig. 3-3). When analyzing the abundance data set, the grouping of canal and river data points and the correlation between axes and landscape parameters remained, although the patterns tended to be weaker (results not shown; three axes, final stress 18.5). Ellenberg values for moisture, light and nutrients were not significantly different between systems (moisture: 6.2 ± 0.06 (Ems) vs. 6.1 ± 0.09 (DEK), p-value = 0.31; light: 6.9 ± 0.04 vs. 6.8 ± 0.04 , p-value = 0.18; nutrients: 6.8 ± 0.09 vs. 6.5 ± 0.09 , p-value = 0.05).

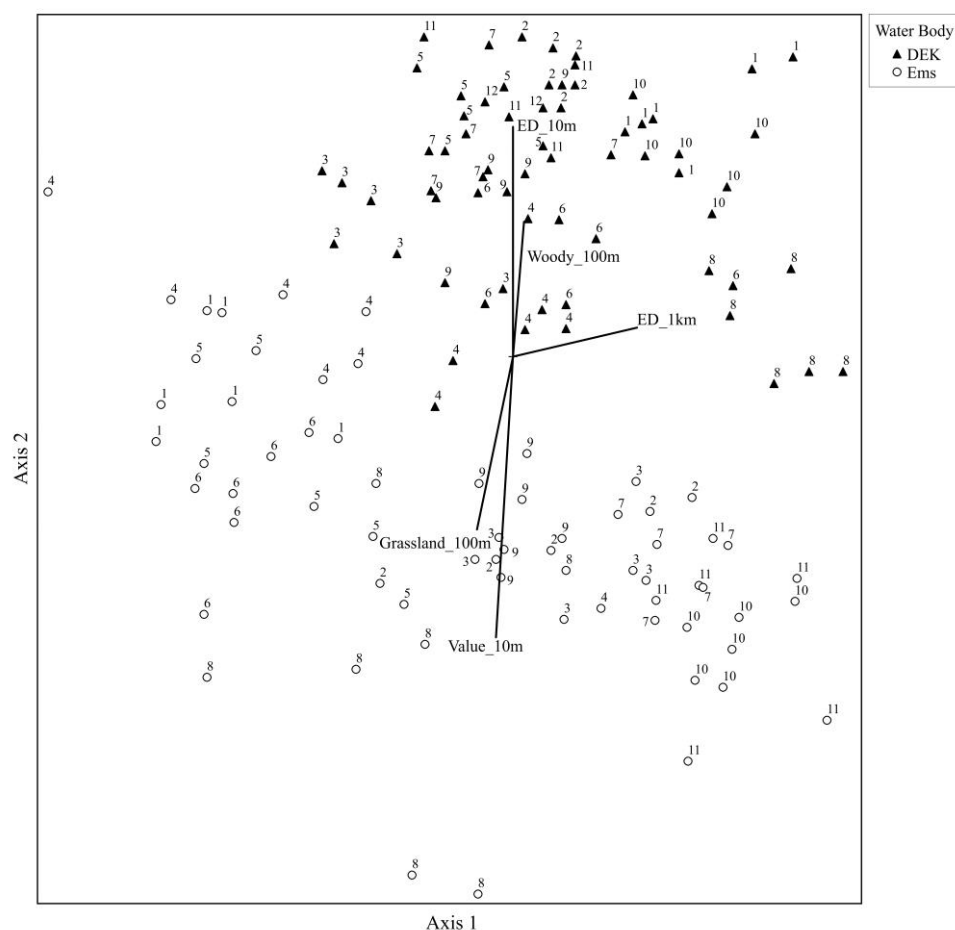


Figure 3-3: Final NMS plot for P/A dataset, axis 1 vs. axis 2 (final NMS with three axes; final stress = 16.96; axis 3 not shown). Every point refers to one sub-transect, numbered by transect. The gain in R^2 is 0.178 for axis 1, 0.443 for axis 2 and 0.150 for axis 3. DEK and Ems plots are separated along axis 2. Environmental variables that correlate with either axis with $R^2 > 0.25$ are indicated in the figure (ED_1 km: $R^2 = 0.290$ with axis 1; grassland_100 m: $R^2 = 0.403$; value_10 m: $R^2 = 0.654$; ED_10 m: $R^2 = 0.537$; woody_100 m: $R^2 = 0.315$, all correlate with axis 2). Refer to Table 2-A2 for a detailed description of the environmental variables.

The difference in spread of relevés in the ordination space is counterintuitively linked to species diversity. While the trend of higher species numbers per relevé along the canal than along the Ems (39.9 ± 2.06 vs. 34.6 ± 2.54 ; fig. 4-4a) was not significant in case of the presence/absence data set, this pattern proved to be significant in case of the abundance data set (canal: 19.4 ± 1.01 , Ems: 15.9 ± 1.31 ; fig. 3-3d). Considering the biodiversity measures Shannon index, Simpson index and evenness, all show higher values for the DEK than for the Ems as well (fig. 4-4). Again, the differences are significant in the

abundance dataset (fig. 4-4d-g). Though not statistically significant, the same pattern is recognizable in the P/A dataset (fig. 4-4a-c).

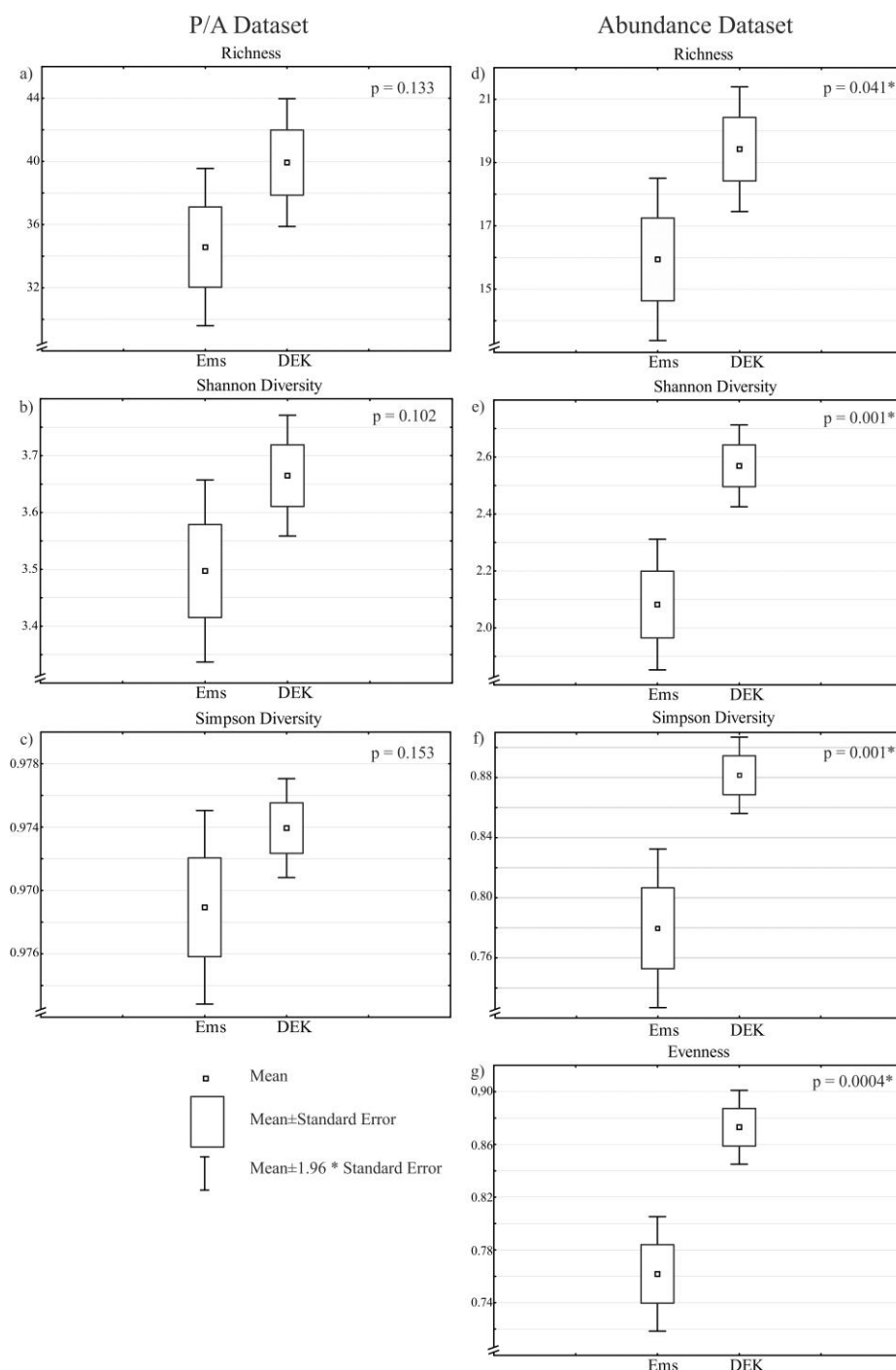


Figure 3-4: Results of t-test for species diversity measures. Species richness, Shannon diversity and Simpson diversity were compared between DEK and Ems separately for P/A dataset (a-c) and abundance dataset (d-f). For presence-absence data, abundance was set to 1 for all species in the calculation of Shannon and Simpson diversity. Evenness was calculated for abundance data only (g). Significance level was $p < 0.05$. In the abundance

dataset, the differences are significant. Please note: Different scales for y-axes are used between figures for better legibility. Y-axes do not start at zero.

As expected from the clear grouping of Ems and DEK relevés in the NMS, indicator species analyses of the P/A-dataset revealed a large number of indicative species for both systems (DEK: 29; Ems: 21; tab. 3-1; abundance data DEK: 11; Ems: 5). As a general pattern the proportion of ruderal species is higher along the EMS than the DEK (tab. 3-1). Species of mesic grasslands are almost exclusively indicative for the vegetation along the canal. A higher percentage of the Ems indicator species (for P/A data) are adapted to humid site conditions with an Ellenberg humidity value greater 7 compared to the DEK (39 % vs. 20 %). Four of the Ems species indicate regular flooding (DEK: 2) and five are indicators for alternating water levels (DEK: 4).

In general, the indicator species for the DEK reflect the composition of man-made habitats along the canal banks: perennials closest to the water, rip rap (e.g., *Rubus spec.*), mesic grassland (e.g., *Arrhenatherum elatius*) and road margin (e.g., *Taraxacum sect. ruderalia*), while the Ems indicator species comprise a higher number of habitats occurring in natural floodplains (e.g., *Salix* dominated alluvial forests).

The NMS result of a higher variability in the vegetation data along the Ems is in part corroborated by the analyses of the functional diversity measures. These also show a wider spread in the Ems data set compared to the DEK data set, i.e., functional dispersion (FDis), functional divergence (FDiv) and Rao's quadratic entropy (RaoQ) are, except in case of FDiv in the abundance data set, significantly higher in the data set from the Ems than in the DEK data set (tab. 3-2). In contrast, functional richness (FRic) and Evenness (FEve) do not differ significantly between the DEK and the Ems.

Table 3-1: Results of the indicator species analysis, separated for P/A dataset and abundance dataset. Species with an indicator value (IV) ≥ 25 and a p-value ≤ 0.05 (Monte Carlo randomization test) were considered indicator species. EM = Ellenberg moisture.

	Species	EM	CSR	P/A		Abundance	
				IV	p-value	IV	p-value
DEK	<i>Rubus fruticosus</i>	5	c	65.9	0.0002	51.2	0.0002
	<i>Taraxacum sect. ruderalia</i>	5	csr	60.6	0.0002	--	--
	<i>Calystegia sepium</i>	6	c	56.4	0.0002	58	0.0004
	<i>Rubus caesius</i>	x	c	56	0.0002	--	--
	<i>Equisetum arvense</i>	x~	cr	54.9	0.0002	47.2	0.0002
	<i>Phragmites australis</i>	10	cs	54.7	0.0002	--	--
	<i>Galium aparine</i>	x	cr	53.9	0.0002	44.6	0.003
	<i>Rumex acetosa</i>	x	c	50.9	0.0002	--	--
	<i>Poa pratensis</i>	5	c	50.6	0.0002	43.3	0.0002
	<i>Plantago lanceolata</i>	x	csr	48.6	0.0002	33	0.002
	<i>Agrostis stolonifera</i>	7~	csr	48.1	0.0008	--	--
	<i>Holcus lanatus</i>	6	c	47.7	0.0002	35.4	0.006
	<i>Arrhenatherum elatius</i>	x	c	45.9	0.0010	35	0.029
	<i>Eupatorium cannabinum</i>	7	c	41.9	0.0036	29.7	0.010
	<i>Solanum dulcamara</i>	8~	c	41.7	0.0002	--	--
	<i>Holcus mollis</i>	5	csr	39.4	0.0002	--	--
	<i>Iris pseudacorus</i>	9=	cs	37	0.0044	--	--
	<i>Carex hirta</i>	6~	c	36.4	0.0002	--	--
	<i>Trifolium repens</i>	5	csr	35	0.0022	--	--
	<i>Quercus petraea</i>	5	c	34.8	0.0002	--	--
	<i>Equisetum pratense*</i>	6	csr	34.1	0.0002	--	--
	<i>Festuca rubra</i>	6	c	32.5	0.0004	25	0.016
	<i>Epilobium hirsutum</i>	8=	c	32.4	0.0032	--	--
	<i>Geranium robertianum</i>	x	csr	32	0.0002	--	--
	<i>Vicia angustifolia</i>	x	cr	31.9	0.0002	--	--
	<i>Acer pseudoplatanus</i>	6	c	30.4	0.0002	--	--
	<i>Bromus sterilis</i>	4	cr	30.4	0.0002	--	--
	<i>Valeriana dioica*</i>	8	csr	27.2	0.0008	--	--

Table 3-1 (continued)

	<i>Glyceria maxima</i>	10	cs	25.3	0.0006	--	--
	<i>Dactylis glomerata</i>	5	c	--	--	49.5	0.042
Ems	<i>Artemisia vulgaris</i>	6	c	58.8	0.0002	46.5	0.0002
	<i>Impatiens glandulifera</i>	8=	cr	57.5	0.0002	52	0.0002
	<i>Cirsium vulgare</i>	5	cr	51.2	0.0002	61.5	0.0002
	<i>Tanacetum vulgare</i>	5	c	48.1	0.0002	--	--
	<i>Erysimum cheiranthoides</i>	5	cr	45.5	0.0002	--	--
	<i>Carduus crispus</i>	6	cr	45.2	0.0002	--	--
	<i>Atriplex prostrata</i>	6	s	41.1	0.0002	--	--
	<i>Salix fragilis</i>	8=	c	39.4	0.0002	--	--
	<i>Lamium album</i>	5	csr	38.3	0.0002	--	--
	<i>Salix alba</i>	8=	c	36.4	0.0002	--	--
	<i>Sisymbrium officinale</i>	4	cr	35.7	0.0008	36	0.0004
	<i>Achillea ptarmica</i>	8	cs	34.8	0.0002	--	--
	<i>Lythrum salicaria</i>	8~	cs	33.4	0.0002	--	--
	<i>Stachys palustris</i>	7~	c	33.1	0.0018	--	--
	<i>Alopecurus pratensis</i>	6	c	32.5	0.0012	--	--
	<i>Myosoton aquaticum</i>	8=	cs	31	0.0108	--	--
	<i>Bromus inermis</i>	4~	c	30.1	0.0002	--	--
	<i>Rorippa amphibia</i>	10	cs	28.2	0.0002	--	--
	<i>Thalictrum flavum</i> *	8~	c	26.4	0.0002	--	--
	<i>Scrophularia nodosa</i>	6	cs	26	0.0002	--	--
	<i>Sinapis arvensis</i>	x	cr	25.8	0.0002	--	--
	<i>Elymus repens</i>	x ~	c	--	--	41.5	0.0132

Table 3-2: Results of t-test for functional diversity measures. Functional richness (FRic), functional evenness (FEve), functional dispersion (FDis), functional divergence (FDiv) and Rao's quadratic entropy (RaoQ) were compared between DEK and Ems separately for P/A dataset (P/A) and abundance dataset (Abun). Significant differences are in bold ($p \leq 0.05$).

			Mean	SE	N	p-value	Konf - 95%	Konf + 95%
FRic	P/A	DEK	0.375	0.024	11	0.593	-0.071	0.117
		Ems	0.398	0.036				
	Abun	DEK	0.031	0.004	11	0.162	-0.025	0.005
		Ems	0.021	0.005				
FEve	P/A	DEK	0.973	0.002	11	0.756	-0.008	0.006
		Ems	0.972	0.003				
	Abun	DEK	0.873	0.005	11	0.635	-0.027	0.017
		Ems	0.869	0.008				
FDis	P/A	DEK	0.217	0.004	11	0.127	-0.003	0.018
		Ems	0.225	0.005				
	Abun	DEK	0.214	0.004	11	0.021	0.003	0.032
		Ems	0.231	0.007				
FDiv	P/A	DEK	0.750	0.007	11	< 0.001	0.019	0.049
		Ems	0.784	0.006				
	Abun	DEK	0.804	0.005	11	0.453	-0.016	0.033
		Ems	0.813	0.008				
RaoQ	P/A	DEK	0.055	0.002	11	0.038	0.000	0.009
		Ems	0.060	0.002				
	Abun	DEK	0.054	0.002	11	0.007	0.003	0.016
		Ems	0.064	0.003				

3.3.2 Landscape patterns

The analysis of the area weighted mean biotope values showed that the proportion of biotopes with a high biotope value (class 4) do not differ significantly between DEK and Ems (mean DEK = $18.6\% \pm 1.55$, mean Ems = $14.5\% \pm 1.3$, p value = 0.08). The proportion of biotopes with a high to very high value (class 4 and 5 combined) is significantly higher for the Ems than for the DEK (DEK = $24\% \pm 1.86$, Ems = $38.6\% \pm 2.55$, $p < 0.0001$). Although too small to analyze statistically, the proportion of habitats under protection by the European Habitats Directive (92/43/EEC, The Council of European Communities, 1992) supports this pattern. Along the DEK dataset, only 3 of 29 1 km-stretches contained protected habitats, whereas every 1 km-stretch of the Ems comprised at least one or more protected habitats. The main types, apart from “water courses of plain to montane levels” (3260), were “riparian mixed forests” (91F0), “alluvial forests” (91E0) and “Luzulo-Fagetum beech forests” (9110). For landscape structure, the richness of biotopes is significantly higher (fig. 3-5a) along the Ems than along the DEK. The Shannon diversity index on landscape level does not differ significantly between both systems (fig. 3-5b). Evenness is higher at the DEK areas (fig. 3-5d). Consequently, dominance is higher at the Ems (fig. 3-5c).

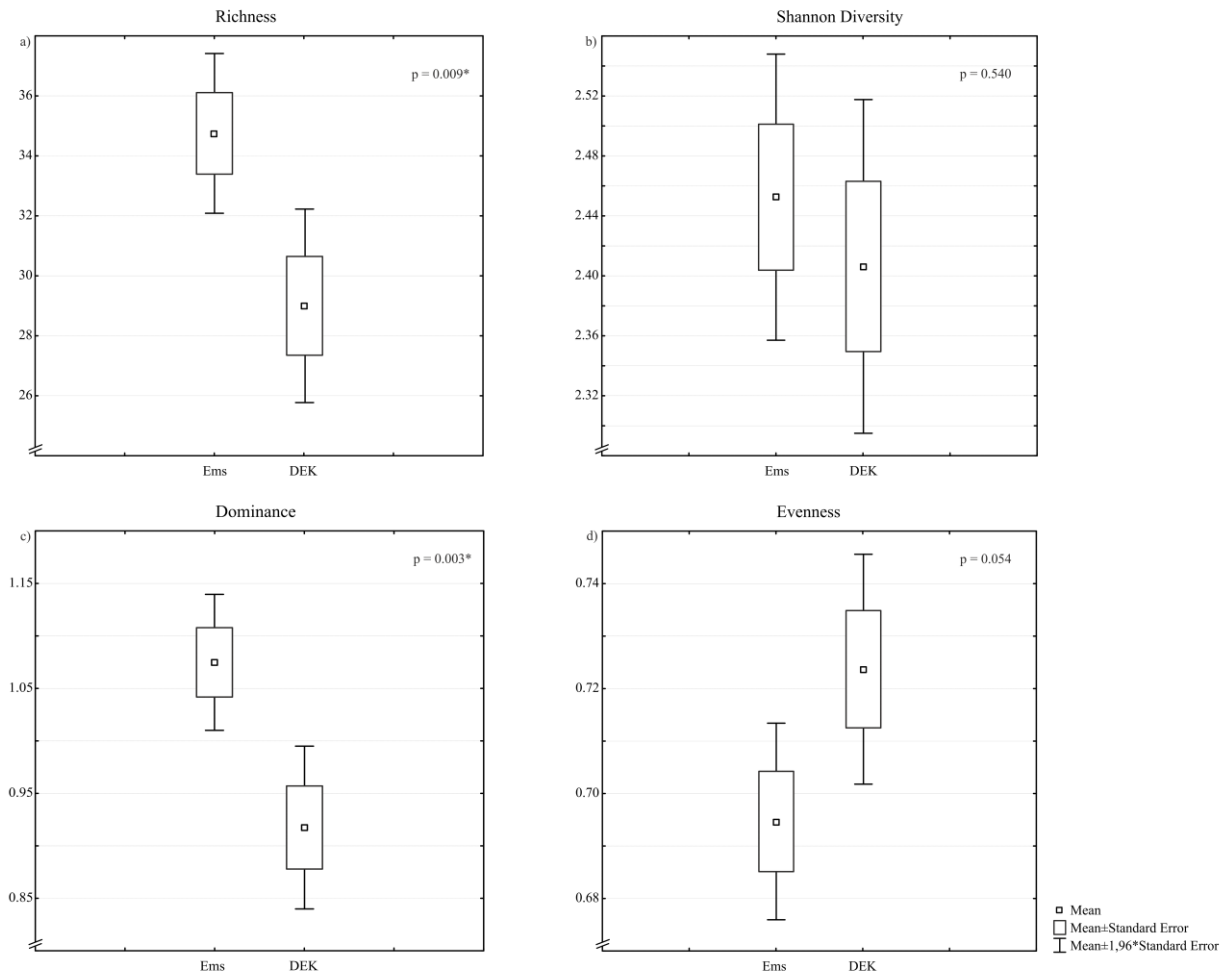


Figure 3-5: Result of t-test for landscape structure diversity measures ($p \leq 0.05$). Please note: Different scales for y-axes are used between figures for better legibility. Y-axes do not start at zero.

3.3.3 Landscape effects on biodiversity

We calculated regression trees for the total dataset (fig. 3-6a), as well as for the Ems and DEK transects separately (fig. 3-6b,c). The analysis relates Shannon species diversity to edge density, a measure of landscape structure, and to land cover patterns, as represented by the proportion of arable land, grassland, woody vegetation and settlements within 1 km from the sample transects. The regression tree for the total dataset used 9 splits (10 terminal nodes) and resulted in an R^2 of 0.675. The variables that remained in the tree construction were arable_1km, aspect, distance_weir, ED_10m, ED_1km, NP_1km, value_10m and settlement_1km. Variables that were not included in the final model were those directly related to vegetation, such as cover or canopy height, as well as land use in the closer vicinity (100 m buffer) or productivity. The first split according to differences in edge density (ED_10m) results in an almost complete separation of the data set into an

Ems dataset (left-handed, 58 Ems vs. 6 DEK sub-transects), and a DEK dataset (right handed; 60 DEK vs. 8 Ems sub-transects). When analyzing the two datasets separately the Ems regression tree (fig. 3-6b) remained quite similar to the left branch of the regression tree across systems (fig. 3-6a), while the DEK regression tree (fig. 3-6c) showed a lower similarity to the right branch of the complete analysis. The main difference of the Ems tree from the complete tree was an additional split according to the herb cover. The tree for the DEK transects was constructed using the variables edge density and proportion of grassland and woody vegetation, while the right branch of the complete tree comprised edge density, the proportion of settlement, number of patches within 1 km, and aspect.

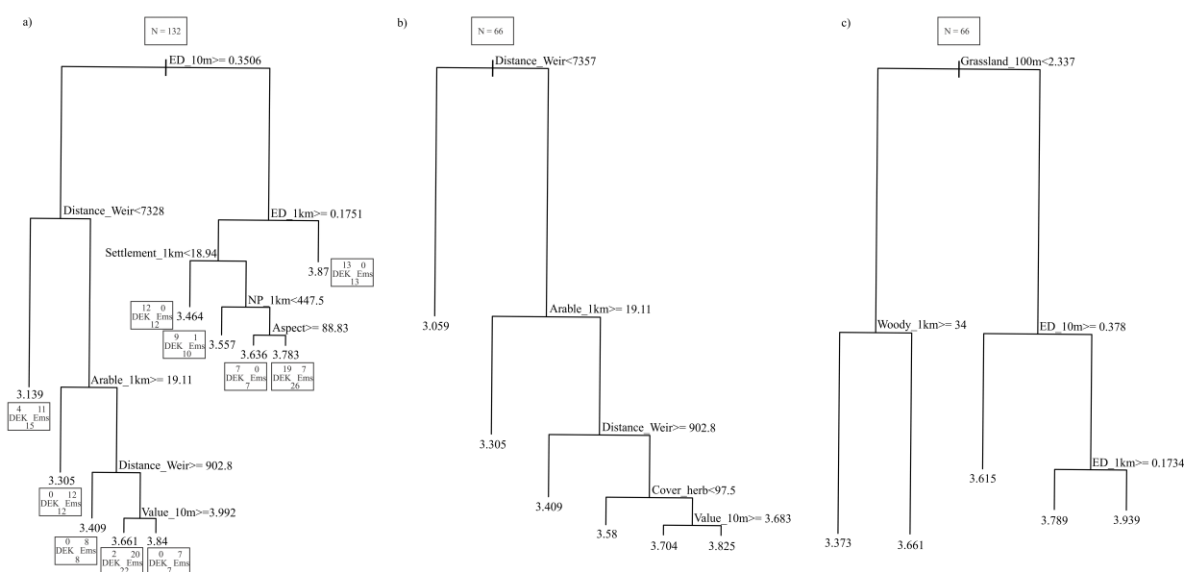


Figure 6: Result of regression tree analysis of all sub-transects (a; N=132), of Ems sub-transects (b; N=66) and of DEK sub-transects (c; N=66). Follow split values to the right. Terminal leaves are labelled with the mean group value. In figure a, the boxes below the leaves contain the total number of cases in the respective group and the number of cases belonging to DEK or Ems within the group. Total dataset: $R^2 = 0.675$. Ems dataset: $R^2 = 0.716$. DEK dataset: $R^2 = 0.640$. Refer to tab. 3-A2 for a detailed description of the environmental variables.

3.4 Discussion

While differences in emergent vegetation between regulated and unregulated rivers have been frequently studied (e.g., Poff and Zimmerman, 2010; Kennedy and Ralston, 2012), the emergent vegetation along artificial waterways has been neglected so far (Chester and Robson, 2013). In the present study, the NMS and indicator species analyses revealed general differences in species composition between river and canal banks. While most of the DEK indicator species are competitors or generalists, Ems indicator species include a higher proportion of ruderal and stress strategists. This suggests a better adaptation to stress and resource limitations of the Ems vegetation (Grime, 1979), as expected for riparian habitats with high disturbance frequency (Nilsson *et al.*, 1989). Similarly, the indicator species along the river are more adapted to wet site conditions and flooding than those along the canal. This shift in species composition toward more terrestrial species has been widely recognized when comparing natural and regulated or channelized rivers (e.g., reviewed by Poff and Zimmerman, 2010; Oswalt and King, 2005) and is mainly attributed to differences in flow regime (Poff and Zimmerman, 2010) and flooding frequency (Deiller *et al.*, 2001). These general patterns of compositional change seem valid across regions and even continents (Dynesius *et al.*, 2004), while species composition of riparian habitats is site-specific and might not be comparable between regions. Although we found more species with high moisture values along the Ems also the DEK indicator species comprehended some wetness indicators (especially within the high forb and reed stands) and several floodplain species that were also recorded by Goulder (2008) and Willby and Eaton (1996) along British canals. Interestingly, the occurrence of *Epilobium hirsutum*, *Iris pseudacorus* or *Glyceria maxima* in the latter study was higher in backwaters without disturbances by traffic. In our study, these species showed high indicator values for the DEK, which is subject to intensive shipping traffic. The species' diametrical occurrence might be related to differences in the construction of banks between the DEK and the canals studied by Willby and Eaton (1996). They relate the proportion of emergent vegetation to shallow habitats and the steepness of banks, so the DEK banks probably provide more suitable habitat conditions. Further, the numbers of Red List species did not differ significantly between DEK and Ems sites.

These differences in species composition are also related to differences in biodiversity measures between both water bodies. All biodiversity indices analyzed in the present case study showed higher values for the DEK than for the Ems although natural floodplains are considered to be among the most species-rich ecosystems in Europe (e.g., Tockner and

Stanford, 2002). However, a high biodiversity has also been recorded in the few other studies concerning emergent vegetation along canals (Willby *et al.*, 2001; Willby and Eaton, 1996). For diversity patterns along disturbed and natural rivers, studies report contrasting results. While Chipps *et al.* (2006) and Poff and Zimmerman (2010) found that disturbance and flood alteration led to losses in species richness and diversity, Dynesius *et al.* (2004) could not demonstrate differences in richness between regulated and unregulated rivers. Deiller *et al.* (2001) showed that richness in an unflooded (detached from floodplain) alluvial forest was higher than in a flooded alluvial forest since flooding-intolerant species were introduced to the system. While this is in accordance with our results for the canal, their finding that dominance was lower in flooded (more natural) sites is in contrast to our results which indicate higher dominance for the Ems study site.

In contrast to diversity measures, functional richness and evenness do not differ significantly between DEK and Ems. Since functional diversity also takes complementarity of functions between different species into account (Díaz and Cabido, 2001), we assume that several species are redundant in their functional traits, so functional richness does not increase with species richness. Species diversity and functional diversity do not necessarily follow the same trends since functional redundancy may buffer losses in taxonomic diversity (Mayfield *et al.*, 2010). While functional richness and evenness did not differ significantly, functional divergence, dispersal and Rao's quadratic entropy were significantly higher at the Ems. These measures indicate more specialist species (Kotowski *et al.*, 2013) and are related to a high degree of niche differentiation, which lowers competition for available resources (Mason *et al.*, 2005). A higher functional divergence is connected to increased competition and therefore may alter ecosystem functions even at landscape scale (Kotowski *et al.*, 2013).

The pattern of higher evenness and consequently lower dominance along the canal was not only found for species diversity, but also for landscape structure diversity. Biotopes are more evenly distributed along the DEK, since it is an artificially constructed waterway with a controlled hydraulic regime and only little disturbance (Hatcher *et al.*, 1999). The canal is characterized by a uniform longitudinal pattern and small-scale lateral changes between habitats (compare Section 2.1), which is reflected in a high edge density. The richness of biotopes is higher for the Ems which is characteristic for rivers that have been subject to only little anthropogenic alteration (Ward, 1998). In general, landscape structure (edge density and number of patches) and land use patterns (proportions of land use types in the surrounding landscape) play the most important role for species and biodiversity

distribution (e.g., Méndez-Toribio *et al.*, 2014; Allan, 2004). Land use intensity is an indicator for anthropogenic disturbance intensity. Lower intensity (e.g., forestry vs. intensive agriculture) causes fewer negative edge effects (e.g., nutrient or pesticide runoff) on the adjacent biotopes (Méndez-Toribio *et al.*, 2014). Further, different land use types can increase the local species pool from which species can reach the study sites, thus increasing local species richness (Liu *et al.*, 2013). We found evidence for this along the canal where occasional tree seedlings from the surrounding forests got established.

The diversity of floodplains is caused by heterogeneity of habitats and environmental factors (Stromberg *et al.*, 2010). Lower richness and diversity are more related to structural uniformity than to the natural or artificial origin of water bodies (Bolgagni *et al.*, 2013). Doua *et al.* (2012), however, state that heterogeneity does not necessarily lead to higher plant species richness, but that it could even decrease richness at a local scale. Species distribution is not only related to environmental factors but also to other spatial processes, such as dispersal limitation (Doua *et al.*, 2012). In our case study, higher richness of biotopes along the natural water body Ems did not correlate to higher species richness or diversity. In contrast, species diversity was linked to the small-scale lateral fragmentation of the DEK. Habitat heterogeneity is, in our data, reflected by a high edge density (indicative for the lateral fragmentation pattern). The higher evenness for species as well as for biotopes reflects the longitudinal uniformity and lacking dynamics of the canal. Landscape heterogeneity, in our case the high edge density along the DEK, drives not only biodiversity distribution, but also species allocation, as reflected in NMS.

Regression tree analysis showed that the species diversity between DEK and Ems is driven by different factors for the respective water body. For the Ems the main influencing factors are land use, i.e., the proportion of arable land, and the distance to the next weir, which probably reflects anthropogenic disturbance (Beauchamp and Stromberg, 2008). To a lesser degree, the cover of the herb layer and the ecological value of the adjacent biotopes are influencing biodiversity distribution. A high vegetation cover is, at least in our study area along the Ems mostly related to high forb stands with only few dominating species, thus decreasing diversity (Moelder and Schneider, 2011). Reeds and high forb stands are intrinsically species-poor, but still of a high conservation value and they are protected by the German Federal Nature Conservation Act (§ 30 BNatSchG, 2013) and the Habitats Directive (The Council of the European Communities, 1992).

For the DEK, biodiversity distribution is positively related to edge density, which is a surrogate for landscape heterogeneity (see above). According to Kumar *et al.* (2006), edge

density within a small buffer radius has the strongest influence on species diversity. Further, biodiversity is related to the proportion of forest and grassland in the landscape. This finding reflects the impact of land use patterns, which influence biodiversity (1) since more habitat types add more species to the landscape (e.g., Liu *et al.*, 2013) and (2) since land use intensity relates to disturbance intensity and negative edge effects (e.g., Méndez-Toribio *et al.*, 2014).

Nowadays most large rivers are regulated and thus degraded (Wolter 2001). Since restoration to a more natural state is still not adequately applied, human-made waterways such as canals can, at least partly, compensate for some losses. Our results show that the DEK provides habitat for several endangered (Red List) floodplain species, and it shows higher species diversity. However, the species assemblage consists mainly of generalists that are not adapted to the natural riparian regime of frequent disturbances, like the ruderal and stress tolerant species that are indicative of the assemblage along the Ems. Thus, the canal can serve as a habitat only for those floodplain species that are not dependent on the dynamics of a floodplain system. Furthermore, the high landscape heterogeneity, which is the main driving factor for the high species diversity along the canal, is not related to natural dynamics, but to the artificial structuring of the banks. According to Stromberg *et al.* (2010), natural floodplain assemblages are not necessarily species-rich, but their mesoscale pattern provides room for many different functional types. This is reflected in the higher structural richness and the higher functional divergence of the Ems sites. Higher species diversity does not necessarily indicate naturalness, a high ecologic value or functionality (Deiller *et al.*, 2001). Actually, functional diversity is the more important driver for ecosystem functions (Woodcock *et al.*, 2011; Tilman *et al.*, 1997). The intrinsic value of the biotope types along the Ems is reflected in the high amount of valuable habitats and their Habitats Directive status.

Natural or semi-natural rivers are by themselves protected by the Habitats Directive (92/43/EEC, The Council of European Communities, 1992), depending on their ecological status and accompanying vegetation (e.g., Annex I habitat types 3260 “Water courses of plain to montane levels with the *Ranunculus fluitans* and *Callitriche-Batrachion* vegetation” and 3270 “Rivers with muddy banks with *Chenopodium rubri* p.p. and *Bidens* p.p. vegetation”). It is thus not possible for canals to reach a comparable status. However, when considering the definition of habitat in Article 1f) of the Habitats Directive “habitat of a species means an environment defined by specific abiotic and biotic factors, in which the species lives at any stage of its biological cycle” (92/43/EEC, The Council of

European Communities, 1992), and relating this to Article 1i) of the Directive “The conservation status will be taken as favourable when: there is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis” (92/43/EEC, The Council of European Communities, 1992), this leads to the conclusion that a canal, if it provides space for endangered species or protected habitat types like e.g., semi-natural grass-lands or alluvial forests, can indeed reach a ‘favourable’ conservation status. Management schemes that aim at providing sufficient habitat space could therefore help increasing the ecological status of canals.

The higher diversity in landscape structure as well as the higher overall value of biotopes and higher number of protected habitats that occur now along the river show that the DEK, in its present state, can substitute only a limited portion of ecosystem functions offered by an active floodplain system. This is not surprising since the functionality of riparian systems depends on a dynamic flow regime (Poff *et al.*, 1997, in Alfredsen *et al.*, 2012), which an artificial canal lacks.

The banks of the canal form a novel or emergent ecosystem since species composition is related to their man-made habitats. They form azonal systems, which, in contrast to natural rivers with a floodplain as a buffer, are directly connected to the surrounding zonal habitats. Since it is, in most cases, not feasible or even possible to change this man-made ecosystem back to a natural state, their existence and value should be acknowledged and any development actions should focus on the ecosystem services that they provide (Hobbs *et al.*, 2006, 2009). For management strategies, the most appropriate remediation approach is to work within the given limitations of an artificial waterway (i.e., the constructed bank structure and the adjacent land use cannot be changed due to economic reasons) with the aim to maximize functional diversity (Callow, 2012), since it is more closely related to ecosystem functionality than species biodiversity alone (Tilman *et al.*, 1997; Woodcock *et al.*, 2011).

Since the DEK already provides habitat for single endangered floodplain species, a focus on the protection of this habitat function should be the most feasible approach. An example would be an adapted mowing regime as already applied in the existing management scheme for the DEK (BfG, 2006). Chester and Robson (2013) suggest a moderate management of “benign neglect”, which may allow for some natural succession, at least in areas where endangered species that could be threatened by succession are absent. We follow their suggestion since we believe that some natural succession might add to structural diversity and ecological value along the DEK.

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Appendix

Table 3-A1: Traits used for functional diversity analysis, their short name, the reference database from which the traits were derived, their scale level and the specific coding. For binary coding, 1 indicates that trait does apply, 2 indicates that trait does not apply.

Trait	Short Name	Reference	Scale	Specifics
Guild	LifeForm	BiolFlor	Categorical	Woody, herbaceous, grass, sourgrass, fern, legume
maximum height	CanHeight	LEDA	Numerical	In meters
Life Span	LifeSpan_annual	BiolFlor	Binary	Annuals (one flowering phase)
	LifeSpan_perenn	BiolFlor	Binary	Perennials (more than one flowering phase)
Hemeroby	Hem_a	BiolFlor	Binary	Ahemerob
	Hem_o	BiolFlor	Binary	Oligohemerob
	Hem_m	BiolFlor	Binary	Mesohemerob
	Hem_b	BiolFlor	Binary	B-euhemerob
	Hem_c	BiolFlor	Binary	A-euhemerob
	Hem_p	BiolFlor	Binary	Polyhemerob
Nautochory	Nautochory	LEDA	Binary	
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
Position of regenerative organ	Regeneration	BiolFlor	Categorical	Aboveground, belowground, therophyte, no information

Table 3-A2: Environmental variables used for NMS and regression tree analysis, their short name (used as reference in text and figures) and the respective unit.

Category	Variable	Short Name	Unit
Topography	Aspect	Aspect	Degrees
Vegetation	Cover herb layer	Cov_herb	%
	Cover moss layer	Cov_moss	%
	Cover litter layer	Cov_litter	%
	Cover open soil	Cov_soil	%
	Height tree layer	Hght_tree	m
	Height shrub layer	Hght_shrub	m
	Height herb layer	Hght_herb	m
Water	Water Body	Water	1: DEK, 2: EMS
	Distance from next weir or sluice	Distance_Weir	m
Land Use	Landuse within 100 m buffer radius:		
	Proportion of settlement	Settlement_100m	%
	Proportion of arable land	Arable_100m	%
	Proportion of grassland	Grassland_100m	%
	Proportion of woody vegetation	Woody_100m	%
	Landuse within 1 km buffer radius:		
	Proportion of settlement	Settlement_1km	%
	Proportion of arable land	Arable_1km	%
	Proportion of grassland	Grassland_1km	%
	Proportion of woody vegetation	Woody_1km	%
Productivity	Red Edge NDVI	ReNDVI	Unitless
Structure	Number of patches		
	within transect	NP_within	Numeric
	within 10 m buffer radius	NP_10m	Numeric
	within 100 m buffer radius	NP_100m	Numeric
	within 1 km buffer radius	NP_1km	Numeric
	Edge density		
	within transect	ED_within	m/m ²
	within 10 m buffer radius	ED_10m	m/m ²
	within 100 m buffer radius	ED_100m	m/m ²

	within 1 km buffer radius	ED_1km	m/m ²
Biotopes	Number of biotopes		
	Within transect	N_biotopes_within	Numeric
	within 10 m buffer radius	N_biotopes_10m	Numeric
	Area weighted mean biotope value		
	within transect	Value_in	0 to 5
	within 10 m buffer radius	Value_10m	0 to 5

Table 3-A3: Red List Species, their occurrence along both waterways, and their Ellenberg moisture value und strategy type. 1 indicates occurrence along the respective water body; EM = Ellenberg moisture value; ~ indicates adaptation to alternating water levels; = indicates adaptation to regular flooding; CSR = ecological strategy types according to Grime (1979).

Species	Red List	Occurrence		EM	CSR
	Status	DEK	Ems		
<i>Butomus umbellatus</i>	3	0	1	10~	cs
<i>Caltha palustris</i>	3	0	1	9=	csr
<i>Carex elata</i>	3	1	0	10~	cs
<i>Carex vulpina</i>	3	1	0	8=	csr
<i>Cirsium acaule</i>	2	0	1	3	NA
<i>Cynosurus cristatus</i>	3	1	0	5	csr
<i>Dianthus deltoides</i>	3	1	0	3	csr
<i>Equisetum pratense</i>	2	1	1	6	csr
<i>Galeopsis segetum</i>	2	1	0	4	r
<i>Plantago media</i>	3	1	1	4	csr
<i>Populus nigra</i>	3	0	1	8=	c
<i>Pseudolysimachion longifolium</i>	3	0	1	NA	NA
<i>Sagina nodosa</i>	2	1	0	8~	csr
<i>Salix pentandra</i>	3	0	1	8~	c
<i>Scrophularia umbrosa</i>	3	1	1	9=	cs
<i>Thalictrum flavum</i>	3	1	1	8~	c
<i>Tragopogon pratensis s. orientalis</i>	3	1	0	5	NA

<i>Ulmus minor</i>	3	1	0	x~	NA
<i>Valeriana dioica</i>	3	1	1	8	csr
<i>Verbascum blattaria</i>	R	1	0	3	c
<i>Veronica verna</i>	2	1	1	2	sr

Summary

Rivers and their floodplains are hotspots of biodiversity. In their natural state, they are shaped by dynamic conditions in space and time that are mainly driven by flooding and sediment transportation. Humans have always used riparian systems for their needs. Measures such as river straightening or the construction of barrages and levees have altered the hydraulic conditions and the floodplain landscapes. This results in a significant loss of ecosystem functions, floodplain area, habitat space and thus biodiversity. Nowadays, two thirds of the floodplain area in the Northern part of the world are lost, and only 10 % of the remaining floodplains are in an ecologically functional state. Therefore, the protection of floodplain biodiversity is one of the major concerns of the Convention on Biodiversity.

Especially the German Federal Waterways, i.e. rivers, streams and canals used for shipping traffic, are strongly regulated. To improve the ecological status of these waterways, the management needs to incorporate measures for the protection of floristic diversity. However, it is not known how multiple anthropogenic alterations affect the plant species diversity of floodplains in concert, which are the most important factors, and whether these effects are comparable across regions. Thus, an inventory of plant species composition, diversity, and the most important factors influencing both is needed to develop recommendations for an ecological waterway management.

The main objectives of this work were (1) to inventory the plant species diversity in the floodplains and adjacent areas of the German Federal Waterways and to determine the most important relations between regional differences, anthropogenic influence and phytodiversity; and (2) to draw conclusions for the incorporation of biodiversity demands in waterway management regimes.

In a comparative study (chapter 2), we inventoried plant species composition and diversity in 20 study sites representative for the German Federal Waterways. The study sites comprised upland and lowland river stretches covering a range of anthropogenic alterations.

The aim was to determine which species form the floodplain vegetation of Federal Waterways, how composition and diversity is affected by multiple human influences (e.g. regulation by barrages, bank protection, and shipping traffic) and whether the detected patterns are visible across regions and thus universally valid. While biodiversity patterns

strongly differed between upland and lowland rivers, the anthropogenic influence was visible across all study sites. With increasing human influence, floodplain species were replaced by generalist species adapted to terrestrial conditions, since human alterations often lead to a disconnection of the river and the floodplain and inhibit the natural flooding regime. As a consequence, species richness partly increased within the studied habitats.

Since knowledge on the bank vegetation of canals was scarce, canals were excluded from the comparative study and considered separately in a case study (chapter 3). The aim of this study was to gain knowledge about similarities and differences between natural and artificial waterways (canals), their bank vegetation and biodiversity. Similar to the comparative study, species richness was higher along the canal. The bank vegetation was composed of more terrestrial species while the vegetation along the river contained a higher amount of floodplain species. Accordingly, functional divergence, which is related to a higher ecological niche differentiation, was higher along the river.

The findings of both studies suggest that management should aim to reinstall more natural hydraulic conditions and to reconnect rivers and floodplains to improve the ecological status of the floodplains of German Federal Waterways. On the short term, this might lead to a decrease in species numbers, since the invaded terrestrial species will be affected. However, on the long term, more dynamic conditions will lead to the small-scale pattern of habitats that are the main cause for floodplain biodiversity and that will sustain specialized and often endangered species. Even along artificial or strongly inhibited waterways, a management of benign neglect will allow for succession and thus higher habitat diversity.

Zusammenfassung

Flüsse und ihre Auen sind Hotspots der Biodiversität. In ihrem natürlichen Zustand sind sie von zeitlicher und räumlicher Dynamik geprägt, welche vor allem von Überflutung und Sedimentationsprozessen bestimmt wird. Menschen haben Fließgewässersysteme schon immer für ihre Bedürfnisse genutzt. Maßnahmen wie Flussbegradigungen oder der Bau von Querbauwerken oder Deichen haben die hydraulischen Bedingungen und damit die Auenlandschaften stark verändert. Dies führt zu einem signifikanten Verlust von Lebensräumen, Ökosystemfunktionen, und entsprechend Artenvielfalt. Heutzutage sind zwei Drittel der Auen im nördlichen Teil der Welt verloren gegangen. Nur 10 % der übrigen Fläche befindet sich in einem ökologisch funktionsfähigen Zustand. Aus diesem Grund ist der Schutz der biologischen Vielfalt in Auen eines der Hauptanliegen der Convention on Biodiversity.

Vor allem die Deutschen Bundeswasserstraßen, d.h. Flüsse, Ströme und Kanäle, die für den Schiffsverkehr genutzt werden, sind stark reguliert. Um den ökologischen Status der Wasserstraßen zu verbessern, sollen Maßnahmen zum Schutz der Biodiversität in das Management integriert werden. Allerdings ist nicht bekannt, wie verschiedene anthropogene Einflussfaktoren sich gemeinsam auf die Diversität der Flussauen auswirken, welches die wichtigsten Faktoren sind und ob sich bestimmte Effekte überregional vergleichen lassen. Daher wird eine Bestandsaufnahme der Pflanzenartenzusammensetzung, der Pflanzenartenvielfalt und der wichtigsten Einflussfaktoren benötigt, um Empfehlungen für ein ökologisches Wasserstraßenmanagement zu entwickeln.

Die zentralen Ziele der vorliegenden Arbeit waren (1) die Vielfalt der Pflanzenarten in den Seitenräumen und Auen der Bundeswasserstraßen zu erfassen und die wichtigsten Beziehungen zwischen regionalen Unterschieden, menschlichem Einfluss und der Artenvielfalt zu bestimmen; und (2) Schlussfolgerungen zu ziehen, um den Schutz der Biodiversität in die Managementpläne der Bundeswasserstraßen zu integrieren.

In einer vergleichenden Studie (Kapitel 2) wurden die Artenzusammensetzung und die Artenvielfalt der Vegetation in 20 repräsentativen Untersuchungsgebieten entlang der Bundeswasserstraßen erfasst. Die Untersuchungsgebiete umfassten sowohl Mittelgebirgs- als auch Flachlandgewässer und beinhalteten einen Gradienten von stark regulierten zu wenig beeinflussten Gewässerabschnitten. Die Zielsetzungen waren, die Arten, aus denen sich die Auenvegetation der Bundeswasserstraßen zusammensetzt, zu identifizieren, zu bestimmen, wie Zusammensetzung und Diversität von verschiedenen menschlichen

Einflüssen (z.B. Stauregulierung, Ufersicherung, Schiffsverkehr) geprägt werden und zu erforschen, ob die gefundenen Muster überregionale Gültigkeit haben. Während sich die Muster der Phytodiversität stark zwischen Mittelgebirgs- und Flachlandflüssen unterschieden, war der menschliche Einfluss über alle Gebiete hinweg erkennbar. Mit zunehmender Beeinflussung wurden die Auenspezialisten durch Allerweltsarten, welche an terrestrische Bedingungen angepasst sind, ersetzt, da anthropogene Regulierung oft zu einer Trennung von Fluss und Aue führt und das natürliche Überflutungsregime beeinträchtigt. Als eine Folge dieser Artenverschiebung erhöhten sich teilweise die Artenzahlen in den untersuchten Standorten.

Da das Wissen über die Ufervegetation von Kanälen gering ist, wurden Kanäle aus der vergleichenden Studie ausgeschlossen und separat in einer Fallstudie betrachtet (Kapitel 3). Das Ziel dieser Studie war, Erkenntnisse über die Ähnlichkeiten und Unterschiede zwischen natürlichen und künstlich angelegten Wasserstraßen (Kanälen), ihrer Ufervegetation und ihrer Artenvielfalt, zu gewinnen. Entsprechend den Ergebnissen der vergleichenden Studie waren die Artenzahlen entlang des Kanals höher. Die Vegetation setzte sich aus terrestrischen Arten zusammen, während die Vegetation entlang des Flusses einen höheren Anteil an Auenarten beinhaltete. Demgemäß war die funktionelle Divergenz, welche im Zusammenhang mit einer höheren ökologischen Nischendifferenzierung steht, höher entlang des Flusses.

Die Ergebnisse beider Studien legen nahe, dass das Wasserstraßenmanagement darauf abzielen sollte, natürlichere hydraulische Bedingungen zu schaffen und die Verbindung zwischen Fluss und Aue wiederherzustellen, um den ökologischen Status der Auen der Bundeswasserstraßen zu verbessern. Kurzfristig könnte dies eine Abnahme der Artenzahlen zur Folge haben, da die eingewanderten Allerweltsarten betroffen wären. Langfristig würden dynamischere Bedingungen jedoch zu einem kleinräumigen Muster an unterschiedlichen Standortbedingungen führen, welches die wichtigste Voraussetzung für die hohe Diversität von Auenlebensräumen darstellt und welches die Grundlage für spezialisierte und teils gefährdete Arten bildet. Auch entlang von künstlichen oder stark beeinträchtigten Wasserstraßen könnte eine Reduzierung der Uferpflege Sukzession und damit eine höhere Standortvielfalt fördern.

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Erklärung

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