Institute of Landscape Ecology and Resources Management
Division of Landscape Ecology and Landscape Planning
Justus-Liebig-University Giessen

Land-cover change and the distribution pattern of natural and semi-natural alluvial vegetation remnants along the Upper Danube River

INAUGURAL DISSERTATION

for the degree of
Doctor agriculturae (Dr. agr.)

submitted to the
Faculty 09
Agricultural Science, Nutritional Science, and Environmental Management
Justus-Liebig-University Giessen

presented by
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born in Jiangsu, China

Giessen, 2019

With permission from
the Faculty 09
Agricultural Science, Nutritional Science, and Environmental Management
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Contents

List of Publications[1]

1. Xu, F.; Otte, A.; Ludewig, K.; Donath, T.W. & Harvolk-Schöning, S. (2017). Land cover changes (1963–2010) and their environmental factors in the Upper Danube Floodplain. *Sustainability 9*, 943.

2. Xu, F.; Harvolk-Schöning, S.; Horchler, P. J.; Ludewig, K.& Otte, A. (2019). Factors determining the distribution pattern of floodplain vegetation remnants along the Danube River between Straubing and Vilshofen. *Tuexenia 39* (accepted).

Author's contribution:

1. In the first publication I had the main responsibility, including the pre-processing of the aerial images, statistical analysis and paper writing. Dr. Sarah Harvolk-Schöning and Dr. Kristin Ludewig helped me with the data analysis and revised the manuscript. Prof. Dr. Dr. habil. Dr. h. c. (TSU) Annette Otte gave valuable comments on the manuscript. PD. Dr. Tobias W. Donath commented on the manuscript.
2. In the second publication, I had the main responsibility, including the study design, data analysis and paper writing. Dr. Peter J. Horchler provided me with the vegetation data and helped me with the statistical analysis. Dr. Sarah Harvolk-Schöning, and Dr. Kristin Ludewig gave me valuable suggestions on the study design and revised the manuscript. Prof. Dr. Dr. habil. Dr. h. c. (TSU) Annette Otte gave valuable comments on the analysis of the vegetation data and the manuscript.

[1] Citation styles and formatting in the dissertation follow the rules of the respective journal.

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1. Synthesis

In this chapter, the background, objectives and the framework of this thesis are introduced. Furthermore, an overview of the two manuscripts, the main results and conclusions are presented.

1.1 Introduction

1.1.1 Situation of European floodplains

Natural factors in floodplains

Due to the dynamic nature, floodplains are among the most biologically productive ecosystems on earth and provide a complex mosaic of diverse habitats (Ward et al., 1999; Tockner & Stanford, 2002). Natural disturbances of the floodplain vegetation are caused by the hydrological regime (e.g., flood frequency and duration, groundwater amplitude and substrate porosity). They affect the species distribution, dispersion and abundance, as well as the nutrient cycling within floodplain habitats and control floodplain micro-topography through deposition and erosion (Schnitzler, 2008; Gurnell, Bertoldi & Corenblit, 2012; Marks, Nislow & Magilligan, 2014). Natural disturbance processes are primarily responsible for sustaining the high level of heterogeneity, which is manifested in a diverse array of landscape elements and processes. These include longitudinal, lateral and vertical gradients in geomorphic features, surface and subsurface flows of water and nutrients, and disturbance regimes (Ward et al., 2002). The stress and the availability of resources vary along these gradients (Huston, 1994), which also structure the floodplain habitats (Craft, 2015). Distinctive plant communities can often be found at predictable locations along the hydrological gradients (Junk et al., 1989).

As an essential habitat in floodplains, riparian forests strongly depend on the flood pulses for primary productivity, biodiversity, and functioning (Schnitzler, 2008). They can adapt to dynamic conditions and are affected by the hydrological alterations via direct (e.g., physiological tolerance) and indirect (e.g., competition) ways (Dister, 1983; Townsend, 2001; Richards & Hughes, 2007; Marks, Nislow & Magilligan, 2014). The interactions between hydrological regimes, geology, landform, climate and the local species pool are essential preconditions forming the structure and distribution of floodplain forests (Marks, Nislow & Magilligan, 2014).

Human disturbances in floodplains

Floodplain habitats have been altered not only by natural hydrological regimes but also by anthropogenic activities such as river regulation, intensive land use and hydropower plants (Nilsson et al., 2005; Schnitzler, Hale & Alsum, 2005; Hein et al., 2016). Driven by strong human interventions, up to 90% of European floodplains got lost, or are no longer able to prevent floods and provide diverse habitats (Freeman et al., 2003; Tockner et al., 2009; Leyer et al., 2012). The human-induced alterations in floodplains have led to the degradation of water quality and the alterations of terrestrial and aquatic communities (Nilsson & Jansson, 1995). The high biodiversity in the river ecosystems is dramatically reduced, native riparian forests are lost, and the plant species adapted to natural disturbances are faced with extinction (Müller, 1998; Skagen et al., 2005). Over 90% of the European alluvial forest types disappeared, and the remaining forests are in critical conditions (Hughes, 2003). They occur only as small fragments with pristine species composition or as large complexes with altered species composition (Dister et al., 1990). For example, the growth rate of floodplain forests along the Middle Danube was reduced after 1992 due to the upstream Gabcikova Barrage (Somogyi et al., 1999). The EU Habitats Directive (92/43/EEC 1992) and other regulations have been carried out to conserve the extent and quality of the residual alluvial forests.

As an essential anthropogenic modification to control flooding, to facilitate navigation and to make use of hydropower, river regulations including the constructions of dikes, dams, and embankments alter the physical and ecological structures of floodplains (Philippi, 1996; Leyer, 2005). Approximately 77% of the total water discharge of the 139 largest rivers worldwide were strongly or moderately regulated and fragmented by dams (Dynesius & Nilsson, 1994). Dams disrupt organism dispersal, sediment dynamics and alter riverine species composition and abundance (Renöfält, Jansson & Nilsson, 2010). Since the 1940s, hydropower plants have been built to fulfill the rising energy demand (Müller, 1995). Hydropower production has transformed rivers fundamentally by fragmenting river channels and altering river regimes (Renöfält, Jansson & Nilsson, 2010). In many European floodplains, river engineering has accelerated the disappearance of riparian forests (Décamps et al., 1988). In recent years, the coordinated implementation of EU legislation, such as the Water Framework Directive (Directive 2000/60/EC, WFD) and the Floods Directive (Directive 2007/60/EC, FD), has provided the policy framework for river management. In Germany, the most important federal law for water legislation is the Federal Water Act (Wasserhaushaltsgesetz, 2009), which linked the national water acts to the European provisions (BMU, 2016).

Besides river regulation, agricultural land use through intensification of agricultural management and the expansion of arable land causes the loss of semi-natural habitats and biological assemblages, affects the species composition and richness of communities (e.g., floodplain grasslands; Weiner et al., 2011). Until 1950 a traditional way of low-intensity management contributed to the species richness in floodplain grasslands (Selinger-Looten et al., 1999; Warthemann & Reichhoff, 2001), whereas the characteristic floodplain grassland species disappeared under the increasing management intensity (Bischoff et al., 2009). Since the 1950s, floodplain grasslands in Central Europe have been steadily transformed from traditional meadows and pastures into sites of higher productivity used as grassland or – if suitable – as arable fields (Krause et al., 2011, Wesche et al., 2012). For instance, habitat types of typical floodplain grasslands disappeared and have become endangered. Therefore some types are protected by the EU Habitats Directive (e.g., floodplain meadows of the *Cnidion dubii*, Council Directive 92/43/EEC, habitat type 6440).

Apart from the agricultural intensification, extractive industries (e.g., mineral extraction) has added the pressure on the floodplains, and altered the floodplain landscape as well as vegetation (Kondolf, 1997; Wood & van Haselma, 2008). Although gravel mining exposes the subsurface water table and can be a disturbance factor for riparian vegetation, the gravel ponds can provide habitats for fish and native riparian communities in contrast (Roelle & Gladwin, 1999). The topsoil-stripping step returns the substrate to a nutrient-poor condition, where less competitive plants may establish. The extraction activities also create habitats for specialized pioneer species, which depend for germination on patches of open soil created by disturbances. The original habitats of these species were within natural floodplains, where flood dynamics created open sites periodically (INULA, 2015).

During the last decades, changing priorities in the rural and environmental policies, such as the EU nature legislation (e.g., the Habitats Directive) and agriculture legislation (e.g., the Common Agricultural Policy), have encouraged the reappraisal of land management in floodplains from the perspective of nature conservation (Rouquette et al., 2009). The EU Habitats Directive ensures the conservation of a wide range of rare, threatened species and habitat types. The Rural Development Regulation (RDR, Council Regulation (EC) No1257/1999) provides payments to compensate farmers for income losses due to the establishment or restoration of floodplains (Dworak, 2007). The EU Common Agricultural Policy (CAP, Council Regulation (EC) No 1782/2003) has influenced and encouraged the expansion and intensification of agriculture (Wood & van Haselma, 2008). In the Agenda 2000 reform of the CAP, the environmental conditions were attached to the agricultural subsidies to promote proper land management practices (e.g., less intensive farming) in functional floodplains (Moss & Monstadt, 2008).

As explained above, rivers and floodplains are strongly altered by anthropogenic disturbances. As a holistic indicator of the intensity of human disturbances (Jalas, 1955; Sukopp, 1972; Kowarik, 1988), the concept of hemeroby is often used to assess human-induced transformation of phytocoenoses and ecosystems (Sukopp, 1972; Kowarik. 1988; Grabherr et al., 1995; Jackowiak, 1998; Fanelli et al., 2006). It measures the distance between current vegetation and the constructed state of self-regulated vegetation without human interventions (Reif & Walentowski, 2008; Walz & Stein, 2014). Besides that, hemeroby can be also applied to landscapes or habitats in landscape-based analyses, as an indicator for the ecological value as well as the degree of human transformation (Goldsmith, 1975; Steinhardt et al., 1999; Zebisch et al., 2004). At the habitat or landscape level, hemeroby quantifies the disruption of habitat or landscape by anthropogenic activities (Jalas, 1955). At the species level, hemeroby characterizes the disturbance of the optimal and self-regulated habitat for the species, which vary according to whether they benefit from or are harmed by the human interventions (Kowarik, 1988; Hill et al., 2002). Therefore, hemeroby is adopted in land-use investigations since disturbance is strongly related to land use and land-use changes (Zebisch et al., 2004).

Human influences on floodplains at different scales

The scaling issue is especially apparent in floodplains due to the variations in the riverine systems: variation in time (e.g., seasonal or episodic floods or droughts) and variation in space (e.g., landscape patterns) determine the variation among organisms (e.g., size, mobility, trophic roles; Wiens, 2002). At spatial scales, floodplain vegetation can be influenced by both broad-scale physiographic patterns and fine-scale variations for example in soils or terrain (Turner et al., 2004). Human modifications of hydrological processes disrupt the dynamic equilibrium existing in the free-flowing rivers, and alter both the broad- and fine-scale geomorphic features which also constitute habitats for the riparian species (Poff et al., 1997). Large rivers flowing through different eco-regions experience various land-forms, soils and climatic conditions, all of which provide a coarse-scale filter for species pools and relative dominance (Baker & Barnes, 1998). At the fine scale, variations in precipitation and temperature as well as soil characteristics such as texture, pH, and nutrient concentration influence floodplain vegetation considerably (Streng et al., 1989; Jones et al., 1994).

The temporal factors are equally important as spatial scales for the understanding of human impacts. There is a time lag (e.g., relaxation time; Diamond, 1972) between causal events or processes (e.g., forest clearing, agricultural intensification) and biological responses (e.g., species extinction; Nagelkerke et al., 2002; Anderson et al., 2010). The responses of populations and communities to landscape change (e.g., habitat fragmentation) may delay in time (extinction debt, Tilman et al., 1994; colonization credit, Cristofoli et al., 2010). For example, the historical landscape patterns have more influences than the current landscape patterns on the present species diversity in Swedish grasslands (Lindborg & Eriksson, 2004). Temporal dynamics of land-cover change (e.g., the sequence of land-cover types, duration of land-cover type, frequency of land-cover changes, and magnitude of the difference between land-cover types) may interact with various ecological characteristics (e.g., generation time, population size and phenology) to influence biotic responses (Watson et al. 2014). Therefore it is necessary to consider the human influences on the floodplain vegetation on a range of scales.

Landscape patterns in floodplains

All the natural and human disturbances interact with the determination of the landscape patterns in the floodplains (Selinger-Lotten et al., 1999; Gurnell & Petts, 2002). The landscape patterns can be characterized by two aspects: landscape composition (e.g., the element types) and landscape structure (e.g., the spatial arrangement including shape and connectivity of elements; Gustafson, 1998; Wiens, 2002). Typical landscape elements such as sandy banks, softwood forests, hardwood forests, natural levees and marshland present the floodplain naturalness (Baptist et al., 2004). The landscape composition affects population dynamics and persistence by direct effects on reproduction and mortality; landscape configuration influences population dynamics indirectly via effects on among-patch movement (Fahrig & Nuttle, 2005). The responses of organisms to landscape patterns are determined by their morphological, behavioral and life-history traits (Wiens, 2002).

The landscape composition in floodplains refers to the relative amounts (e.g., presence, absence, relative proportions) of each habitat or land-cover type within river corridors (Ward et al., 2002). The compositional variables represent the dominance, relative richness and diversity in the landscape, which affect the floodplain vegetation (Turner, 1989). For example, the patch size affects the vegetation structure of floodplain forests due to the habitat availability or variation in abiotic conditions (Ranney et al. 1981; Hanson et al. 1990; Chen et al. 1999; Crouzeilles et al., 2014). However, landscape composition cannot stand alone without reference to the spatial distribution of habitat types, or the landscape structure, due to their joint contributions (Lamy et al., 2016).

Landscape structure can be characterized by the spatial patterns (e.g., shape, position) of habitats. The shape complexity of habitats determines the boundary irregularity, which might affect the species richness and diversity (Honnay, 2002; Walz, 2011; Moser et al., 2012). Natural landscapes are normally characterized by irregularly shaped units with less distinct boundaries, whereas human activities introduce distinct boundaries to landscapes, with rectangularity and rectilinearity, producing regular shapes with straight borders (O'Neill et al., 1988; Moser et al., 2012). Patch shape affects the number of edges and interior habitats. Edge-driven variations of abiotic conditions have direct impacts on the spatio-temporal distribution and dynamics of species, and they alter the species interactions (e.g., predation, competition, seed dispersal; Murcia, 1995). The edge effects constitute abiotic and biotic changes, and they are especially obvious, when the patches are irregularly shaped (Forman & Godron, 1986), or when the boundaries between natural and modified habitats are sharp (Laurance & Yensen, 1991). In floodplains, the edge structure of riparian habitats caused by the natural disturbance and human activities modifies the accessibility and the permeability of the ecotone (Tabacchi et al., 1996). Therefore, landscape structure plays a key role in species composition of floodplain vegetation (e.g., floodplain forests, Dzwonko, 1993; Bellemare et al., 2002; Turner, 2004; Honnay et al., 2005; Glaeser & Wulf, 2009). Furthermore, landscape structure affects landscape connectivity, which is the degree to which the landscape facilitates or impedes movement among resource patches (Taylor et al., 1993; Goodwin & Fahrig, 2002). Inter-patch distance has the strongest negative effect on the landscape connectivity; however, the habitat amount and fragmentation could affect landscape connectivity negatively or positively (Goodwin & Fahrig, 2002). Habitat connectivity in floodplains is linked to the diversity of indigenous species, and promotes the establishment and spread of neophytes and archaeophytes (Deutschewitz, 2001; Walz, 2011).

Land uses (e.g., agriculture, forestry, and infrastructure) alter the landscape structure and cause fragmentation in all landscape types (McGarigal & Cushman, 2002). In general, habitat fragmentation increases habitat isolation, which can affect the day-to-day movements of a given species (Saunders, 1980), the dispersal of juveniles (Cooper & Walters, 2002), the development of metapopulations (Hanski & Simberloff, 1997), and the large-scale movements of species such as seasonal migration or range shifts in response to climate change (Soulé et al., 2004). River valleys are favored as infrastructure pathways (e.g., waterways, roads, railways) because they connect human settlements built close to rivers. Floodplain fragmentation caused by roads, pipelines and land clearing can impair the ability of organisms to move across floodplain patches or landscapes, with potential effects on species diversity, richness, and the community structure (e.g., composition, trophic organization; Weins et al., 1985; Robinson et al., 1992; Haddad et al., 2015; Wilson et al., 2016). It can also change the microclimate at local and regional scales, which further influences biodiversity (Young & Mithchell, 1994; Didham & Lawton, 1999; Laurance et al., 2011). The fragmentation-mediated processes affect species responses at different levels (e.g., population, community, and ecosystem; Haddad et al., 2015).

1.1.2 Objectives

Given the spatio-temporal heterogeneity of the floodplain landscape and the differentiated response mechanisms of plant species to changing conditions, the general objective of this work is to analyse the human influences on the floodplain landscape and vegetation distribution at temporal and spatial scales. Previous researches about landscape change in a long time span in the floodplain were done at a coarse scale (e.g., 1 km^2) or were conducted as case studies (Butler et al., 2013; Pechanec et al., 2015). There have rarely been studies which analysed the floodplain land-cover change at a detailed scale. Most studies related the distribution of floodplain vegetation either at a broad scale (e.g., flow regulation; Nilsson et al., 1997; Friedman et al., 1998) or at a local scale (e.g., soils; Johnson, 1994; Härdtle et al. 2006). However, the connections between the landscape pattern and floodplain vegetation have rarely been studied. We detected the landscape change at a fine scale (1: 5000) and integrated the landscape pattern, especially the landscape structural parameters, in the analysis of vegetation distribution in floodplains. This thesis aims to answer the following questions:

(1) How did the human activities change the floodplain landscape over time (1963-2010)?

(2) How do the human activities affect the floodplain vegetation at different scales (from the landscape level to the local level)?

(3) How do the landscape changes affect the distribution pattern of floodplain vegetation?

Land cover changes (1963–2010) and their environmental factors in the Upper Danube Floodplain (Chapter 2)

In Chapter 2, we detected the landscape changes in the Upper Danube Floodplain between Regensburg and Vilshofen. Aerial images were interpreted to quantify the changes of landscape pattern from 1963 to 2010. We focused on typical floodplain habitats, i.e., riparian forest, floodplain grassland, arable land. Landscape metrics were selected to quantify the landscape structure. A transformation matrix was used to describe the conversion between land cover types quantitatively and reflect the dynamic of land cover change. We conducted the Classification and Regression Trees (CART) to explore the relationship between environmental factors and land cover change.

The specific research questions of this study were: a). How did the land cover pattern, i.e., the land cover composition and structure, change from 1963 to 2010 in the Upper Danube Floodplain?

b).Which environmental factors are related to land cover change (especially grassland and riparian forest changes) in the active Upper Danube Floodplain? c).Which are the ecological consequences of the recorded trends in a floodplain context?

Factors determining the distribution pattern of floodplain vegetation remnants along the Danube River between Straubing and Vilshofen (Chapter 3)

To understand the human influences on the floodplain vegetation from a comprehensive view, we analysed 108 vegetation relevés collected in the Danube Floodplain in Germany. We explored the relationship between the species composition and environmental variables from the landscape level to the local level with Non-metric Multidimensional Scaling (NMDS), Boosted Regression Trees (BRT) and Classification and Regression Trees (CART).

The specific research questions of this study were: a). How are plant species composition, landscape pattern, and environmental variables related in the Danube Floodplain? b).In floodplains under strong human influences, where are the habitats for species groups located?

1.2 Study area

The study area (Fig.1.1) is located between Regensburg and Vilshofen (River-km: 2,379–2,245) along the Upper Danube in Bavaria, Southern Germany. The Upper Danube between the Black Forest and the Devin Gate below Vienna is characterized by a steep gradient of 0.2-1.1‰ and a flow velocity of 8-9 km/h (Schiemer et al., 2004). The study area is located in the landscape unit "Dungau", which refers to the Danube Valley with very fertile soils and intensive agricultural use between Regensburg and Vilshofen (lfU, 2011). The floodplain landscape in this area contains 254 species of endangered plants, 79 species of endangered birds and other precious species (Schaller, 2007). In this region, most of the natural vegetation has been replaced by agricultural land and settlements. Nowadays, the lowland area is covered by intensively used agricultural land, permanent grassland, and remnants of forests (lfU, 2011). Soils in this area are nutrient-rich, high-yielding cambisols and luvisols (lfU, 2011). It is under a temperate climate with a mean annual temperature of 8°C and a mean annual precipitation of 816 mm (DWD, 2012). The prevailing natural vegetation (PNV) in the study area is alluvial hardwood forest characterised by *Fraxinus excelsior* and *Ulmus minor* (*Fraxino-Ulmetum* (Tx. 1952) Oberd. 1953) in complex with softwood forest elements (e.g., *Salix alba*; *Salicetum albae* Issl. 1926; Seibert, 1968).

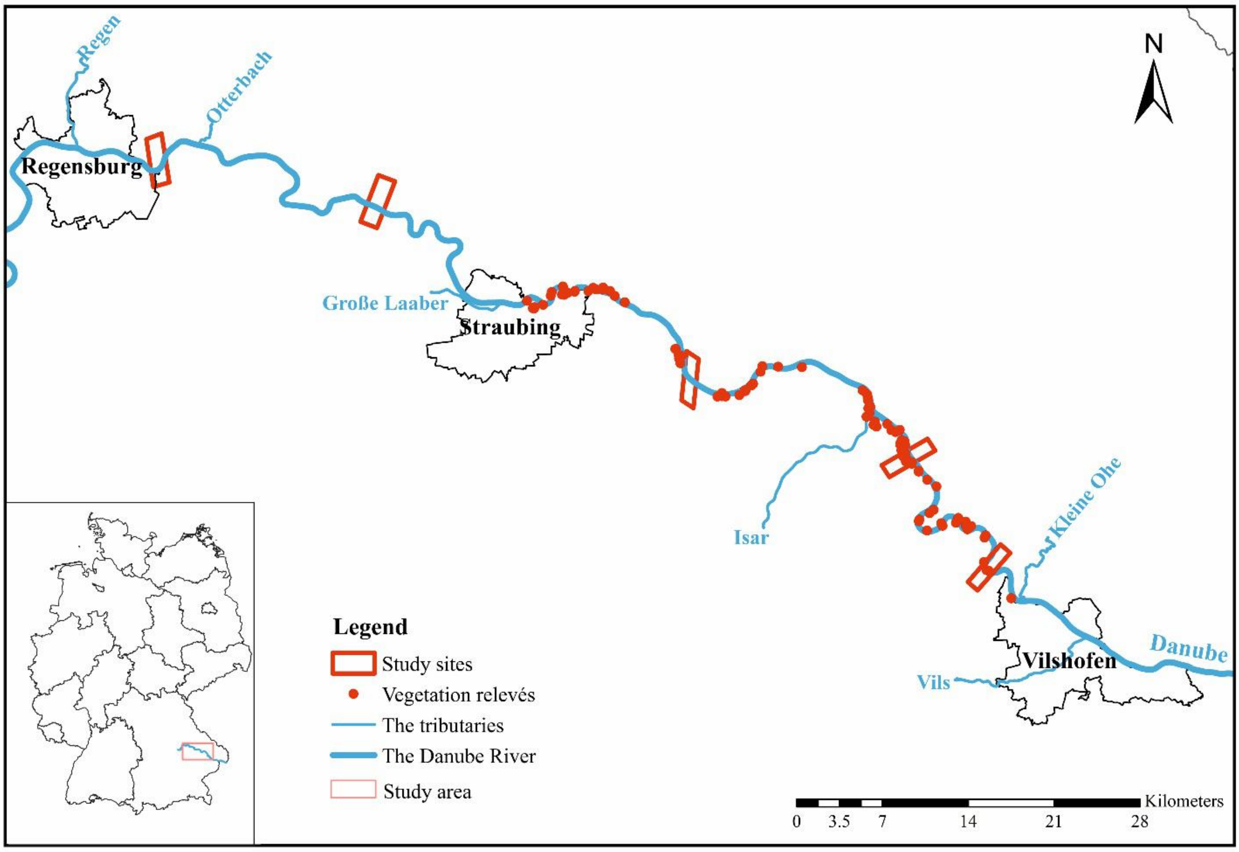

Fig.1.1 Location of the study region and sites (Source: Germany map: VG250 (Administrative boundaries 1: 250,000), provided by the Federal Agency for Cartography and Geodesy (BKG, 2007); Study sites (Chapter 2): in Barbing, Gmünd, Irlbach, Niederalteich and Langkünzing respectively; Vegetation relevés (Chapter 3): data collected in the context of "Variantenunabhängige Untersuchungen zum Ausbau der Donau zwischen Straubing und Vilshofen" by the German Waterways and Shipping Administration (BfG, 2013); the shapefile of the Danube was provided by BfG; the tributaries were manually digitalized based on the Bing Maps Aerial in 2012 (30 cm resolution; © 2012 Microsoft Corporation)).

The loss of hydrological ever-changing floodplains along different sections of the Danube varies from 73% to 95% (95% in the Upper Danube, Schneider et al., 2009), which mainly results from the human interventions such as channelization, flood protection measures and construction of hydropower plants (Demek et al., 2008). The high population density and industry establishment in the catchment area has led to water pollution. The prevailing land use in the Danube Floodplain is arable land (about 52%), followed by settlement/traffic and grassland (Brunotte et al., 2009, 2013). The EU farming policies since the 1960s and the national subsidies have encouraged the agricultural development in the Danube Floodplain and the intensification of crop and animal production (ICPDR, 2003 & 2016). In other large floodplains of Europe and worldwide, river regulation and engineering formed morphological changes. In the Upper Danube, the river engineering has started during the 19^{th} century to improve navigation, flood control and agricultural drainage (Schiemer et al., 2004). The 69-km segment from Straubing to Vilshofen (River-km 2,318-2,249) in the study area (between Regensburg and Vilshofen) is one of the few free-flowing parts of the Danube in Bavaria without dams.

1.3 Methods

1.3.1 Analysis of the landscape pattern (Chapter 2 & Chapter 3)

To obtain the historical and recent land-cover data, I manually digitalized the aerial images in the study area of the years (1963, 1978, 1995, 2010 in Chapter 2 and 2012 in Chapter 3). The land-cover was classified into five primary types: woody vegetation, agricultural land, water, margin, and built-up land, which were divided into various subtypes (Chapter 2 and Chapter 3) according to the characteristics of land-use, structure and vegetation cover. I selected representative landscape metrics both at the class and landscape levels to quantify the landscape composition (e.g., proportion, richness, and evenness) and structure (e.g., shape, fragmentation, and proximity; Chapter 2 & Chapter 3). In Chapter 2, a transformation matrix was used to describe the conversion between land cover types. Hemeroby degrees were assigned to the land use types to quantify the human impact on the landscape (Chapter 3).

1.3.2 Analysis of vegetation data (Chapter 3)

In Chapter 3, 108 relevés were selected in the study area from the AuVeg German floodplain vegetation database (BfG, 2012). Based on transformed species data, cluster analysis (with Bray-Curtis distance and complete-linkage) was applied to identify the species groups. I used the indicator value (IndVal) method (Dufrêne & Legendre, 1997) to select the indicator species, which are ecological indicators of the clusters. Non-metric

Multidimensional Scaling (NMDS) was used as an indirect method to analyse the pattern of vegetation distribution in a multidimensional space.

1.3.3 Analysis of the relationships (Chapter 2 & Chapter 3)

Compared to the linear models, regression tree models perform well in exploring the non-linear relationships and interactions among predictors (Chambers & Hastie, 1992). In Chapter 2, I used the Classification and Regression Trees (CART) to explore the relationship between environmental factors and land-cover change. In Chapter 3, both the Boosted Regression Trees (BRT) and the CART were used to analyse the relationship between species composition, landscape pattern and environmental variables: the BRT showed the relative contributions of environmental variables to the species composition, whereas the CART was used to explore which environmental variables affect the occurrence of a species cluster. All the statistical analyses were performed in R version 3.1.0 (R CORE TEAM 2012) and the workflow of the studies is shown in Fig.1.2.

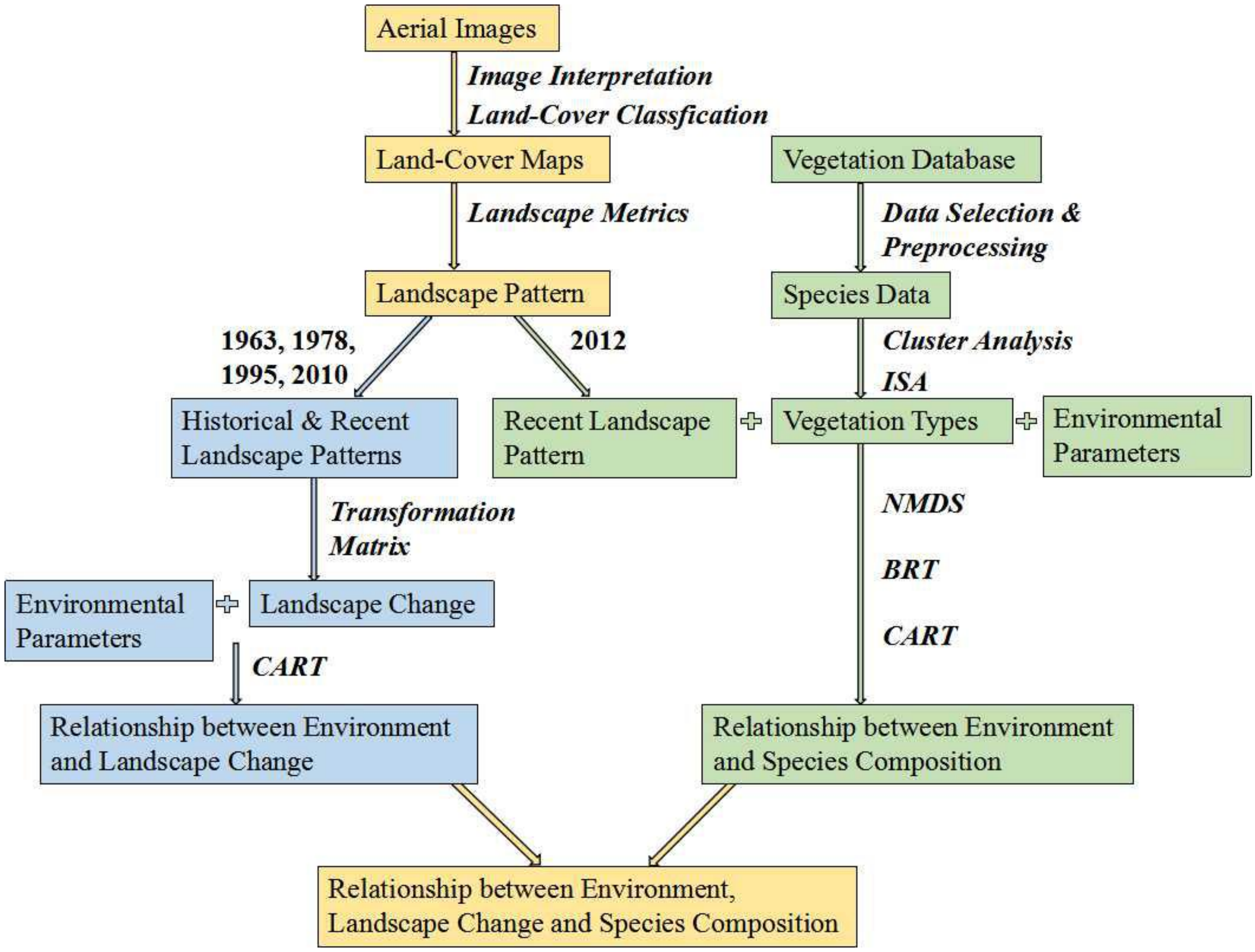

Fig. 1.2 The workflow of the study (Abbreviations: ISA= Indicator Species Analysis, NMDS= Non-metric Multidimensional Scaling, BRT= Boosted Regression Trees; CART= Classification and Regression Trees; Boxes and arrows: blue stands for Chapter 2, green stands for Chapter 3, yellow stands for both Chapter 2 and Chapter 3).

1.4 Main results and discussion

1.4.1 How did the human activities change the floodplain landscape over time (1963-2010)?

From 1963 to 2010, the active floodplain of the Upper Danube experienced increased fragmentation by construction of infrastructure such as roads and paths. The built-up land such as settlements and infrastructure increased. Agricultural land increased in patch size as a consequence of agricultural intensification. The amount of agricultural land in the floodplain was reduced because of the German agricultural policy and the land consolidation policy (Flurbereinigung). Since 2003, with more concerns on biodiversity, water management, and soil protection, the CAP has supported the farmers to adopt sustainable agricultural practices. In Southern Germany, the Bavarian Cultural Landscape Program (KULAP, 2007-2013) subsidized the farmers for the afforestation on agricultural land. Despite the high soil fertility, part of the agricultural land was transformed into riparian forest due to the unreliable water conditions in the floodplain. Nevertheless, the agricultural land still maintained a high share (43.9%) in the active floodplain in 2010.

Not only agricultural land but riparian forest changed noticeably. Although riparian forest gained an overall increase compared to the status in 1963, it lost a little habitat (2.3%) from 1995 to 2010 and was partly converted to grassland. The cumulative loss of riparian forest was driven by dam construction, intensive agriculture, urban development and forest management (Schnitzler et al., 2005). In the study area, river engineering projects between Straubing and Vilshofen after the 1990s altered the riparian habitats. Even along the free-flowing stretch of the Danube, there are still dikes and embankments. In the management practices of German floodplains, the riparian forest was removed to decrease the roughness and to increase the water velocity. Riparian forests along many large rivers were lost or heavily modified by flow regulation and agricultural activities (Scott, 2003), and only relict patches of riparian forest remained (e.g., along the Upper Rhine River; Schnitzler, 1995).

In the study area, loss of floodplain grassland was partly induced by the transformation of permanent grassland into arable land due to land-use intensification. The decline of livestock production and a preference for market crop production after the 1980s contributed to this transformation. The conversion of grasslands to crop fields contributes to the loss of soil organic matter by a seasonal loss of plant cover (inter-cropping periods) and the enhancement of soil respiration through common tillage practices (Huggins et al., 1998; Alluvione et al., 2009). Another part of the floodplain grasslands was converted to riparian forests. This can be explained by the increased inundation duration, and a lower soil quality of these sites (Bren, 1992; Poff et al., 1997). There have been two different trends of changes in European alluvial grasslands since the 1950s (Green, 1990). Agricultural intensification in the lowland areas, indicated by the increased use of machines, fertilizer, cutting and grazing pressure, leads to the extinction of local species (Bastian & Bernhardt, 1993; Gehrig-Fasel et al., 2007). Abandonment of the land unprofitable for agricultural use leads to the encroachments of shrubs and trees into old pastures and cultivated land (Hodgson et al., 2005). Some arable land has been converted to grassland to feed cattle with maize and silage. Both trends resulted in the grassland transformation over time in the study area. In addition, there were 2030 biogas plants in Bavaria in 2010 and the need of grassland biomass for biogas production contributed to the transformation from arable land to grassland (Amon et al., 2005).

Besides the policy incentives, soil quality and topographic parameters were the most important environmental factors affecting the farmers' decisions for the agricultural land in the study area. Grassland in the active floodplain with higher soil rating indexes changed into arable land, while grassland with lower soil rating indexes tended to change into the riparian forest, which confirmed less preference of agricultural production on these soils. The farmers tend to convert the grassland with higher productivity into arable land to improve the agricultural production (Tilman et al., 2002). In this study, riparian forest change was mainly related to height above mean water level and distance to the river. The observed increase of riparian forest especially close to the river and in low heights above mean water level indicated that agricultural land use near the river became de-intensified because high water levels threatened the field cultivation. The flood-dependent characteristic and the preference for high groundwater level of riparian forest allowed these sites to develop into the forest.

The complex temporal trajectories of landscapes in the Upper Danube Floodplain were a consequence of the combination of physical drivers and human influences. Human activities such as flow regulation, agricultural intensification and infrastructure construction altered landscape composition and structure, and modified the ecological communities in floodplains.

1.4.2 How do the human activities affect the floodplain vegetation at different scales?

Even in a human-modified floodplain, the floodplain vegetation is primarily influenced by the river regimes. In the study area, the hydrological parameters (e.g., the mean flooding duration) at the floodplain level were correlated most strongly with the species composition. Hydrology and geomorphology are essential to explaining the vegetative patterns in the wetland (Minshall et al., 1985; Krüger, 2010). Although there are dikes and embankments in the free-flowing stretch of the Danube, the distribution of both woody and herbaceous species groups (e.g., river bank vegetation, floodplain meadows, softwood and hardwood forests) followed the gradient of flooding duration. The species composition changed along this gradient because the species show different flood tolerances, which refer to the species adaptations to variations in depth to the water table and soil texture. For example, the adaptations in trees include morphological (e.g., adventitious roots, stem buttressing, root flexibility) and physiological adaptations (Naiman & Décamps, 1997). The longer inundation durations favor only specialized species (mostly helophytes; Tabacchi et al., 1996). Therefore, the species composition of plant communities at any position in a floodplain reflects local hydrological conditions as well as the flood tolerance of individual species (Capon, 2005).

Besides the natural factors, human activities changed the landscape pattern (Chapter 2) and modified the distribution pattern of floodplain vegetation in the study area (Chapter 3). Landscape pattern is less important than hydrological regimes in determining the species composition. The distribution of vegetation units was comparable to those in natural floodplains; however, there were differences in the sizes and locations of habitats. Despite the typical species composition, some species groups (e.g., softwood remnants) either lost their habitats or occurred in atypical habitats. The habitat of softwood forests was lost due to the infrastructure construction and only remnants in narrow strips remained along the river. Landscapes around the softwood remnants and floodplain meadows were strongly fragmented and were occupied by large proportions of built-up land (e.g., infrastructure, settlements) and agricultural land, which resulted in a high landscape hemeroby. In the study area, roads and other infrastructure were built close to the river where the affected species groups mainly occurred, because floodplains and valleys provided a relatively flat landscape for infrastructure construction (Pennington et al., 2010). In other large floodplains, the transportation infrastructure interrupted the natural disturbance regime, degraded the channel and floodplain habitat structure (Blanton & Marcus, 2013). Besides the infrastructure development, river regulation such as levees, dikes and bank protections limited the species distribution in the study area. As a high-hemeroby species group, the *Glyceria maxima-Persicaria amphibia* group was confined to the banks of backwater and gravel ponds, but not at its typical habitat at the river banks due to the river embankment. The secondary habitats provided by backwater, gravel ponds and other anthropogenic freshwater habitats for the short-lived species were documented in other studies, too (Chester & Robson, 2013; Bubíková & Hrivnák, 2018). Habitat loss and altered location of species groups in the study area reflected the strong influences of human-modified landscape pattern on the floodplain vegetation.

Site land use and soil characteristics at the local level were of minor but measurable importance to the species composition in the study area. Like other large floodplains, the Danube Floodplain was preferred for agriculture because of the naturally high fertility. Site conditions such as the topographical and soil characteristics, as well as previous land uses influence the land management decisions of landowners (Robinson, 2004). Therefore, they are an underlying driver of the landscape pattern affecting the species distribution. In the study area, soil texture varied among species groups. For example, the *Acer pseudoplatanus-Fraxinus excelsior* group grew on the loamy soils, which is typical for hardwood forests. The fine-textured soil with high carbon content and thick, uniform sediments, indicates static flooding conditions (Graf-Rosenfellner, 2016). However, variations of soil texture had little influence on the species composition in the study area, which might be due to the scale issue. Turner et al. (2004) proved that the soil effects on the mature floodplain forest are more obvious at broad spatial scales. The main soil types in the study area were gleyic fluvisols and gleysols-calcaric fluvisols, where the reed vegetation, the mesic meadows, and the shrub species occurred. The mesic meadow was shifted from the traditional habitat with cambisols to the less-preferable areas with gleysols-calcaric fluvisols and gleyic fluvisols. Due to its characteristics (e.g., good structural stability, high porosity, good water holding capacity and internal drainage) and satisfactory fertility, cambisols are preferred in crop production (Driessen et al., 2001). Therefore, the areas available for mesic meadows were limited to those with less-favorable soil conditions. In the land-cover change process of the study area (Chapter 2), the flood-prone areas with low soil rating index were also changed into grassland.

In general, hydrological, landscape structural and soil characteristics were all important to the species composition of floodplain vegetation, which corresponded to the previous findings that the distribution pattern of riparian vegetation was strongly influenced by the species-specific physiologies together with the abiotic (e.g., hydroperiod, landforms, and sediments) and biotic (e.g., competition, life-history) factors (Hupp & Osterkamp, 1985; Nilsson et al., 1989; Hughes, 1990; Scott et al., 2003; Tockner et al., 2003; Naimann et al., 2010).

1.4.3 Combination of temporal and spatial scales: land-cover change and distribution pattern of floodplain vegetation

Influences of landscape-structure change on the species composition and distribution

The landscape in the Danube Floodplain became more fragmented than in the previous status in 1963, which was mainly due to the constructions of roads and other infrastructure. Riparian forests in some study sites became more aggregated from 1995 to 2010, but there were no significant changes of fragmentation degree in riparian forests. In the study area, the softwood remnants along the river were surrounded by dense infrastructure and settlements (Chapter 3). However, the forest's species composition was similar to the composition under more natural conditions. The decreased proximity between grasslands patches indicated the poorer connectivity in floodplain grasslands (Chapter 2). Both types of the floodplain meadows (e.g., the *Agrostis stolonifera-Persicaria maculosa* group & the *Alopecurus pratensis-Taraxacum officinale* group in Chapter 3) showed the typical species composition of floodplain grassland. The species composition of floodplain communities is not totally altered and the vegetation is comparable to the typical floodplain communities that have been described in the literature (Oberdorfer, 1992a, 1992b, 1992c). Thus, the floodplain in the study area is not transformed into a novel ecosystem (Hobbs et al., 2006).

In the study area, fragmentation (e.g., indicated by edge density caused by infrastructure) was related to the species composition (Chapter 3). According to literature, fragmentation may have effects on vegetation and it should be noted that significant responses to fragmentation can be either positive or negative due to the complex mechanisms (e.g., positive: due to higher habitat diversity, positive edge effects, reduced intraspecific and interspecific competition, etc.; negative: caused by higher assumed predation at habitat edges, lower connectivity in landscapes with many small patches than with few large patches, minimum patch size effects, etc.; Fahrig, 2017). No significant effects of habitat fragmentation were also recorded in some studies (Fahrig, 2003, 2013).

Despite the lack of observed influences of increasing fragmentation on the species composition in this study, other studies had the following findings: some changes on the habitat are visible immediately after the construction of a road that fragments the landscape (e.g., shifts in habitat pattern, changes in population sizes, vegetation structure and composition at edges), others may appear in the long term (e.g., genetic related changes on populations, extinction of species with slow life cycles; Benítez-Malvido & Arroyo-Rodríguez, 2008). The species composition in the riparian forest remnants might have been altered by the fragmentation. The reduced fragment size and the increased proportion of edge habitat can cause shifts in the physical environment that lead to the loss of large and old trees in favor of pioneer trees (Haddad et al., 2015). The softwood remnants along the river in the study area are in narrow strips with high edge-area ratios, which could alter and degrade the tree species composition and dynamics (Capon et al., 2013, Stromberg et al., 2013). It was proved that the configuration and size of the fragment may influence the degree of change following fragmentation (Nagy et al., 2015): patches with higher shape complexity may have higher patch colonization and emigrations rates and this can cause greater variability in population size and a decreased probability of population persistence (Collinge & Palmer, 2002); shape complexity accentuates the extent to which edge effects permeate habitat patches, reducing core area for patch specialists (Didham, 2010). These effects are severe for linear patch features such as the strips of remnant vegetation along the rivers, thus the size and configuration of the remnants in the study area might have similarly influenced changes in forest structure and composition. However, riparian ecosystems might be more resilient than other systems because of the inherently heterogeneous environmental conditions (Carpon, 2013). This allows the species and communities to survive perturbations by avoiding them or resisting them, and responding afterwards by recolonizing (Fremier et al., 2015). Therefore, there might be an extinction debt in the study area, and the further fragmentation might become a problem in the future.

Influences of landscape-composition change on species composition and distribution

Land-cover changes caused the habitat loss of riparian forests and grasslands (Chapter 2), and affected the size and extent of some plant communities (e.g., softwood remnants, short-lived species groups, Chapter 3). The infrastructure development in the study area has led to the loss of riparian forest in recent years, which was formerly driven by the land demand for agriculture and settlements. Habitat for riparian forests (e.g., softwood forests) was lost and reduced to the narrow strips. In Chapter 3, only galleries of willows rather than the extensive forests were found along the Danube, but the species composition was comparable to the typical softwood forests. Therefore, the landscape change of the Upper Danube Floodplain led to the loss of critical habitats like riparian forests and floodplain grasslands, but the influences on the species composition could not be clarified in this study.

Land-cover changes in the Upper Danube Floodplain also led to the shift of locations of some species groups. Gravel ponds in the former floodplains had an obvious increase after the 1960s, especially from 1978 to 1995 (Table 2.4, Chapter 2), and the increased construction of gravel ponds provided secondary habitats for the short-lived species group *Glyceria maxima-Persicaria amphibia,* which used to occur on the river banks (Chapter 3). The gravel pits located along the large rivers were formed after World War II due to increasing demand for the gravel–sand material to rebuild the cities (Fľaková et al., 2014). They have a diversity of associated habitats such as marsh, swamp and reed beds. However, gravel mining activities along the other parts of the Danube for the gravel and sand exploitation caused considerable land degradation and biodiversity loss (e.g., in Slovakia, Wood et al., 2000; Mészáros, 2014). In the study area, the construction of gravel ponds in floodplains occupied the space for riparian habitats (e.g., floodplain forest). But they provided secondary habitats especially for the river bank vegetation which lost its original habitat due to the enlargements of river embankment.

We assumed that species composition and distribution might be related to the landscape change, based on the time-lag effect or the species extinction theory. However, land-cover changes (e.g., increased fragmentation, increase of built-up land like roads, agricultural intensification) in the study area along the Upper Danube contributed to the size and location rather than the species composition of the plant communities in the floodplain. Studies that evaluate the influence of landscape change across multiple spatial scales, found that the responses are complex and interacting and vary with location and landform (Allan, 2004).

Another finding is that typical floodplain vegetation could occur even in the floodplains under strong human influences. It might be due to the free-flowing characteristic of this part of the Danube. Although there are dikes and embankments along this part, there have been no dam constructions in recent years. In contrast, the constructions of dam and locks, as well as the land-use changes along the regulated part of the Danube near Donaustauf in Germany, caused the disappearance of many valuable and endangered plant species and communities in 2010 (Glaab et al., 2012). Reduced water level fluctuations caused by the construction of dams and dikes along the Elbe River led to substantial changes in the species distribution and composition in the floodplain (Leyer, 2005). The species composition in floodplain vegetation might stay similar to the previous state. Bragg & Tatschl (1977) found the riverbank stabilization activity along the Missouri River accounted for the increased rate of decline of floodplain forests, however, the species composition was similar to before. At a large scale, the climate change might induce the shifts in the hydrological regime and affect the species composition in floodplains (Thuiller et al., 2005). Wang et al. (2017) found that the species composition of *Salix* was strongly influenced by contemporary climate and historical climate change than habitat heterogeneity at a broad scale.

1.5 General conclusions

Human activities have strong influences on the landscape pattern and species composition in the Upper Danube Floodplain (Chapter 2 & Chapter 3). The species composition of floodplain vegetation in the study area, affected by hydrological parameters, landscape pattern and soil characteristics, was similar to that in the natural or semi-natural state. The distribution (e.g., size, location) of some species groups (e.g., the *Glyceria maxima-Persicaria amphibia* cluster, the *Salix viminalis* cluster, the *Salix alba* cluster) were different from the typical conditions, which could be partly due to the human-induced landscape changes (e.g., more gravel ponds, infrastructure development). Despite the lack of previous vegetation data, the increasing fragmentation might have influenced the species composition and dynamics in the riparian forest and floodplain grasslands.

The reduced extent of floodplain habitats (e.g., softwood remnants) and the shift of locations of typical floodplain communities may lead to the disruption of the natural movement of organisms, which might cause ecological limitations on the survival and evolution of native flora and fauna. The whole study demonstrated how the human activities changed the landscape and vegetation in the Upper Danube Floodplain. The influences of human interventions on the land-cover change as well as the distribution pattern of vegetation remnants, highlight the importance to understand the past and current landscape patterns in the floodplain. The coordination and incentive programs should be developed for farmers and landowners to increase or restore floodplain forests, and to create agricultural land in other areas. The negative impacts of infrastructure development in the floodplains on the riparian habitats and vegetation should be brought to the attention.

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2. Land cover changes (1963–2010) and their environmental factors in the Upper Danube Floodplain

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Keywords: riparian landscape; landscape pattern; landscape dynamics; disturbance

Abstract: To analyze the changes in the Upper Danube Floodplain, we used aerial photos to quantify the change of landscape pattern from 1963 to 2010. We focused on typical floodplain habitats, i.e., riparian forest and floodplain grassland. We used landscape metrics and transformation matrix to explore changes in land cover structure and composition. The active floodplain experienced increasing fragmentation from 1963 to 2010. Despite an increase of aggregation, riparian forest suffered a 2.3% area loss from 1995 to 2010. Arable land in the active floodplain declined by 28.5%, while its patch size significantly increased. Elevation, distance to river and soil quality were the most relevant environmental factors for the land cover change in the floodplain. Higher soil quality or longer distance to river led to an increase of conversion from grassland into arable land; grassland patches with poorer soil quality were likely to change into riparian forest; riparian forest closer to the river and with a lower height above mean water level tended to remain stable. This comprehensive understanding of historical land cover change and environmental factors is needed for the enhancement of landscape functions and sustainable development in the floodplain.

2.1 Introduction

Natural and semi-natural floodplain habitats are valuable but rare. As an essential component of riverine ecosystems, riparian forests would form the Potential Natural Vegetation (PNV) that would theoretically develop without human influence [1,2]. Riparian forests have a high biomass productivity and habitat value. They provide various functions including water storage, water quality improvement, protection against flood and erosion, dead-wood provision for the structural diversity of the river, and they act as a buffer against negative influences of adjacent agricultural and industrial activities [3]. In many European floodplains, riparian forests were reduced or disappeared because of the river management activities. Consequently, riparian forests became threatened floodplain habitats [4].

Floodplain grasslands harbor exceptionally high numbers of species [5]. They experience periodic flooding and they are regularly mown or grazed. Grasslands in floodplains without nature protection measures have experienced alarming losses since the 1950s [6]. This loss is attributed to land drainage, fertilizer uses and the conversion from grassland to cropland [7].

The riparian landscape has changed tremendously over time in various floodplains worldwide [8]. In Europe, the Danube is an example for this: since the beginning of the 19th century, 80% of the Danube Floodplain has been lost due to river regulation, land cover change and dam construction [9]. Compared with other stretches, especially the Upper Danube River has suffered significant modification in the last two centuries [10]. The anthropogenic influence on the Danube River can be clustered into several phases [11]: from the 18th century to the 1850s, meanders were cut off and the riverbed was narrowed to raise the transportation capacity; from the 1850s to 1900, low water regulations for waterway transport and sediment extractions for construction uses were implemented. Land parceling and settlement growth in the 19th century continuously changed the Danube Floodplain [12]. At the beginning of the 20th century, power plants were constructed and more dredging projects followed. Many gravel pits were built along the river from 1950 to 1960 [13]. Flood control, navigation, and hydroelectric power plants caused many problems: alteration of the riverine landscape, degradation of the river bed, decoupling of the floodplain from the river, disturbance of the lateral connectivity and exchange processes, restriction of hydro-morphological dynamics, reduction of habitat variability and biodiversity [14]. Dam construction and river regulation may prevent flooding, cause sediment deficit and change hydro-geomorphic patterns, which further disrupt the composition and structure of riparian vegetation [15,16]. In case of the Danube Floodplain, changes of the ground-water level led to the degradation of forest and other riparian vegetation types [17].

Land cover in the past can control or constrain current land cover composition, and changing trends may affect ecosystem development in the future [18]. Previous researchers have demonstrated the influences of historical land cover structure on the current diversity of plant species [19]. Habitat loss and other environmental changes can cause delayed responses of some species, which is called the extinction debt [20]. The conditions are no longer suitable for the persistence of some plant species, and they will go extinct in the future [19]. However, provided the species persist, there is time to implement habitat restoration and other measures [21]. A clear understanding of land cover change reveals the threats to biodiversity and helps to establish better conservation measures.

From the middle of the last century, the conversion from riparian forest to agricultural land and urban area occurred in Central Europe (e.g., the Middle Elbe River [22]) and worldwide (e.g., the Upper Mississippi River [23], the Laoha River [24], the Willamette Valley [25]). Other riparian land cover types (e.g., grassland, fallow land) were converted to arable and urban land [24]. Conversely, the conversion from other land over (e.g., open land) to woodland led to an expansion of riparian forest in some European floodplains (e.g., the Magra River [26], the Lech River [27]) and worldwide (e.g., the Upper San Pedro River [28]). However, some studies found no fundamental changes in the forest cover, but rather the conversion of agricultural land from extensive permanent grassland to intensive arable land [29]. As a general trend, human influence in most of the floodplains is increasing, which is in conflict with nature conservation [30]. This trend calls for alerts and threatens the need for more natural floodplain landscapes.

The fundamental method to quantify the temporal evolution of land cover is to interpret satellite images/aerial photos [16,26,31]. Landscape metrics, based on the geometry (e.g., number, size, shape and distribution) of patches of different land cover types, have been used to quantify landscape change [32,33]. Researchers selected metrics based on specific categories (e.g., shape, fragmentation, and diversity) [34,35]: Lausch and Herzog [36] selected a few metrics (e.g., MPS (mean patch size) and IJI (interspersion and juxtaposition index)) from various metrics to monitor the landscape structure in Leipzig South region and Espenhaim; Zhao et al. [37] applied fragmentation metrics (e.g., MPS or LPS (largest patch index)), shape metrics (e.g., LSI (landscape shape index)) and diversity metrics (e.g., SHDI (Shannon's diversity index), SHEI (Shannon's evenness index)) to assess the impact of dam construction on the change of landscape patterns in the Lancang River Basin.

Several studies analyzed the influence of environmental factors on the riparian landscape. Topographic variables (e.g., elevation, slope, aspect etc.) were estimated to affect the land cover changes [38]. Climatic gradients, inundation, soil moisture, nutrients and disturbance affect the riparian vegetation [30,39,40]. Within the catchment, elevation and distance from the river in general have the primary influence on the composition and structure of riparian vegetation [41]. Along the lateral gradient, elevation increases from the river channel to the upland and reflects the topographic features in the floodplain (e.g., levees) [41]. However, some studies found the modern forest distribution is decoupled from the natural environmental conditions [42]. In the floodplain landscape with agriculture as the major component, the arable land tends to occur in the coarse-grained natural levee/point bar close to the river channel, where it is infrequently flooded with rapid drainage; however, the pasture land was more associated with the cohesive clayey deposits such as the backswamp, where it is seasonally flooded with poor drainage [31]. Due to the dynamic characteristics of the floodplain, the mechanism of the relationship between environmental factors and the change of floodplain habitats is complicated. Not only the river stage, but also the spatial variability of floodplain geomorphology in the large river system affects the floodplain water table [43].

Although many studies have been conducted about the long-term land cover change in the floodplain, most of them were done at a coarse scale (e.g., 1 km^2) or they were conducted as case studies [29,44]. For example, Jones et al. [45] studied riparian land cover change (1972–2003) across the continental United States at the catchment and riparian scales and they found the decline of natural land cover (e.g., forest) as well as the increase of agricultural and urban land. Since floodplain biotopes are rather small and dynamic, studies at a finer scale are needed to enable a more detailed and accurate understanding of land cover change in the floodplain. To fill this knowledge gap, we used the land cover analysis scale of 1:5000 in our study, which enables a more detailed and accurate understanding of how the land cover in the floodplain changed at the finer scale. The larger number of study sites makes the comparison possible.

The objectives of this study were (1) to determine past land cover pattern of floodplain with regard to the importance for ecological structures and functions; (2) to identify the relationship between environmental factors and land cover change; (3) to assess the observed trends in a floodplain context for a more sustainable floodplain development. We focused on the changes of riparian forest and floodplain grassland owing to their unique importance to the floodplain. Besides a clear understanding of land cover change and the environmental factors, land cover change should be evaluated from an ecological point of view. The following research questions were addressed:

- How did the land cover pattern, i.e., the land cover composition and structure, change from 1963 to 2010 in the Upper Danube Floodplain?
  - How did the grassland pattern change?
  - How did the riparian forest pattern change?
- Which environmental factors are related to land cover change (especially grassland and riparian forest changes) in the active Upper Danube Floodplain?
- Which are the ecological consequences of the recorded trends in a floodplain context?

To conduct a comprehensive and comparable study about the long-term changes in a floodplain, we analyzed the land cover change in the Upper Danube Floodplain in a 50-year time span. We chose this study period (1963–2010) because in the 1950s German agriculture prospered due to a large demand for food after World War II [46]. Since the 1960s, the German agricultural policy has been regulated at a European level. This greatly altered agricultural production methods in Germany, which influenced the land cover change nationwide [47].

2.2 Materials and Methods

2.2.1 Study area

The study area is located along the Upper Danube River in Bavaria, Southern Germany (River-km 2,379–2,245) (Fig. 2.1). The Danube River is an important international waterway, which origins from the Black Forest, passes through ten countries and finally enters the Black Sea; it has a pluvial-nival flow regime. As an essential bio-corridor in Europe and the hotspot of natural habitats, the Danube River is of high research value [48]. The Upper Danube River refers to the part from its source to the confluence with the river Morava at Bratislava (River-km 2,415–1,791). It runs for 587 km through Southern Germany; this part is characterized as mountainous with low water temperature and high flow velocity with an average inclination of the river bed of 0.93% [49].

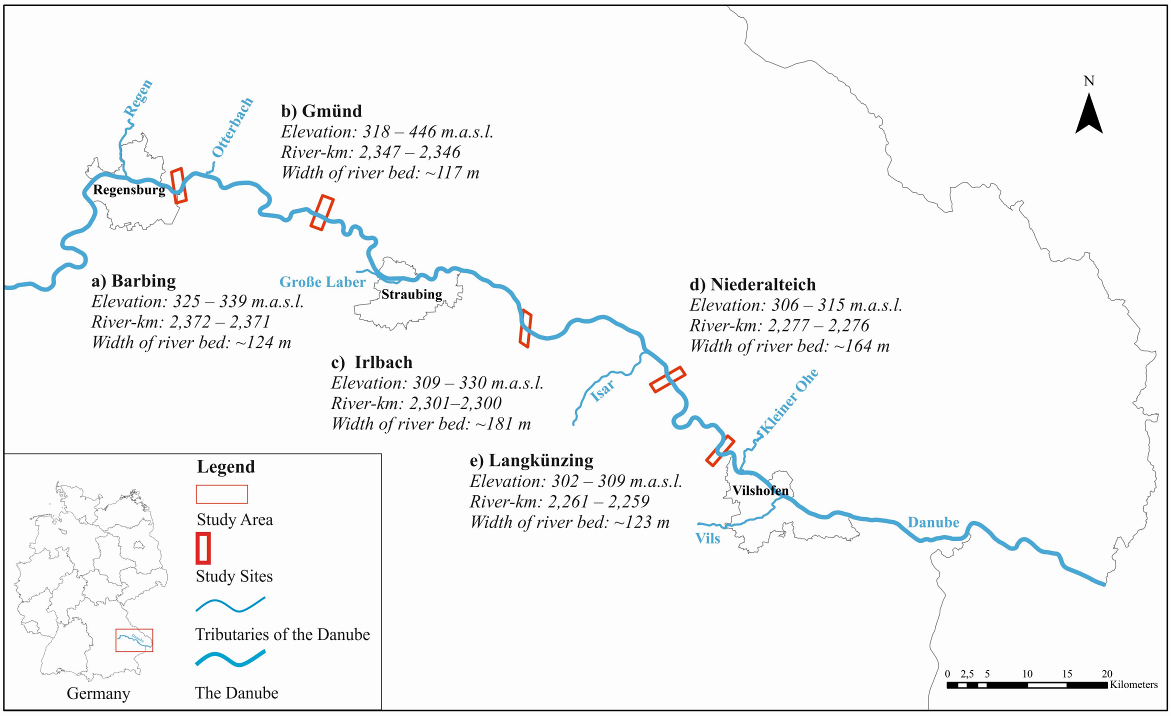

Fig. 2.1 Location of study sites between Regensburg and Vilshofen along the Upper Danube River**.**

In the study area, we choose five study sites randomly: each study site covers approximately 400 ha, comprising the length of 2 km along the river segment and the width of 1 km on each side of the river (Table 2.1). All study sites have a gentle terrain with a mean slope of 1.5° and the mean elevation of each study site is included in Table 2.1. They are situated in the "Dungau" landscape unit in the Danube Valley between the Bavarian Forest and the Lower Bavaria Upland. This region is a cultural landscape with highly fertile and intensively farmed loess plains [50]. The geographical location determines its characteristics: the channel substrates are gravel and crushed stones mostly of limestone from the western Alpine foothills, and the top layer mainly consists of clay or loam with sand in the old meander loops. The predominant soil types are Gleysols, Fluvisols, Cambisols and Luvisols (digital soil data provided by the Bavarian State Office for Survey and Geoinformation (LDBV)). The study sites are under temperate climate with a mean annual temperature of 8 °C and a mean annual precipitation of 816 mm [51].

Table 2.1 Description of the five study sites.

Study Site	Area (ha)	Area of Active Floodplain (ha)	Mean Elevation (m a.s.l.)	Mean Slope (°)	Mean Soil Rating Index *
Barbing	425	203	329	1.0	47.3
Gmünd	422	198	331	1.6	53.1
Irlbach	423	41	319	1.4	59.3
Niederalteich	428	64	310	1.0	53.2
Langkünzing	426	48	305	1.0	53.8

Note: * Definition please see Section 2.3. Abbreviation: a.s.l.: above mean water level.

The river stretch under study is regulated by sluice Regensburg (River-km 2,379), sluice Geisling (River-km 2,354) and sluice Straubing (River-km 2,324); only the river reach between Straubing and Vilshofen is free-flowing. The tributaries joining in this segment are Regen, Vils, Kleine Ohe, Otterbach, Große Laber and Isar. In this study, the active floodplain refers to the part of floodplain periodically inundated by the lateral overflow, and the former floodplain refers to the fossil floodplain outside the actual river dynamics [22].

The PNV in the study area includes alluvial hardwood forest of *Fraxinus excelsior* and *Ulmus minor* in complex with softwood forest elements e.g., *Salix alba* [52]. The softwood forest occurs in the area close to the river, where the main soils are Gleysols, Fluvisols or Cambisols on the carbonate—rich, silty to sandy sediments, or on the sediments with a wide range of grain sizes (digital soil data provided by LDBV). In the higher part and on consolidated terraces of the floodplain with Luvisols or Cambisols on the loess loam sediments, the PNV is the alluvial hardwood forest of *Ulmus minor*, *Fraxinus excelsior* and *Carpinus betulus* [52].

2.2.2 Analysis of land cover composition and structure change

The Land Use and Land Cover (LULC) data in 1963, 1978, 1995 and 2010 were extracted from aerial images (for 2010: orthophotos) at a scale of 1:5000 provided by LDBV [53]. Since it was impossible to collect the aerial images on the same date of the above years, we selected the aerial photos in 1963, 1978, 1995 and 2010 from similar months (May, June and July). We corrected the geometric errors of the historical images. Ground control points (GCPs) and the Digital Elevation Model (DEM with 10 m resolution, provided by the German Federal Institute of Hydrology (BfG)), were used to relate the old aerial photos to the orthophotos in 2010. Based on the pre-processing of the images, we conducted visual interpretation for all aerial photos because it is more suitable to catch the details, e.g., small landscape structures. All figures were interpreted individually with an average minimum mapping unit of 2 m^2. The workflow is given in Fig. 2.2. Other methods like using the NDVI or LAI to determine land use classes require satellite images as input data [54], which were not available for the historical time steps.

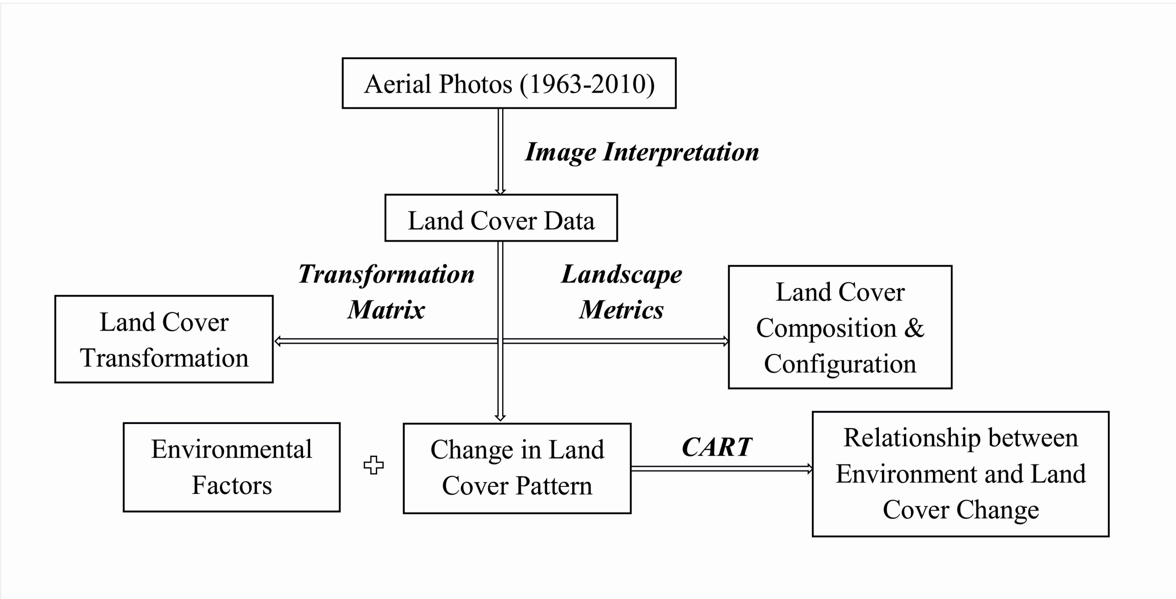

Fig. 2.2 The workflow of the study: the land cover data were derived from the aerial photos, analyzed with transformation matrix and landscape metrics; Classification and Regression Tree Model (CART) analysis was used to explore the relationship between land cover change and environmental factors.

Developing a classification key was the preparatory step for the aerial photo interpretation in ArcGIS 10.2.1 (ESRI, Redlands, CA, USA). According to the surface features, land cover can be classified into five primary groups: woody vegetation, agricultural land, water, margin and built-up land, which were divided into 22 subtypes by specific land-use, structure and vegetation cover (Table 2.2). Riparian forest was defined as the vegetation strip growing next to the water bodies. Margins were defined as one separate group because they are essential ecological corridors.

Table 2.2 Classification of land cover into five types and 22 subtypes.

Type	Subtype	Description
Woody vegetation	Riparian forest	Woodland adjacent to water bodies (e.g., the Danube River, backwater, backwater lake and creek)
	Forest	A complex of trees and other woody vegetation not adjacent to the water body
	Copse	A thicket of trees or shrubs
Agricultural land	Arable land	Land where crops such as maize, wheat and rye are sown
	Grassland	Grass-dominated land mown for fodder production or grazed
	Orchard	Garden with fruit trees close to settlements
Water body	Artificial pond	A gravel pit for extraction of gravel filled with water
	Backwater	A water body periodically or seasonally connected to the main channel
	Backwater lake	A stagnant water body close to and not connected with the main channel
	Creek	A small narrow stream
	Ditch	A long narrow excavation for drainage and irrigation
	River	Danube River
Margin	Field hedge	Closely spaced shrubs and trees in line separating fields from each other
	Field margin	Non-woody vegetation and grass strips in line between fields
	Road hedge	Closely spaced shrubs and trees in line separating roads from adjoining fields or other facilities
	Road margin	Non-woody vegetation and grass strips in line separating road from adjoining fields or other facilities
Built-up Land	Vegetated path	Unpaved path covered with vegetation (e.g., in forest, between fields)
	Path	Paved path with concrete or other surfaces
	Road	Routes with one or more lanes
	Settlements	Houses/homesteads grouped together
	Construction	Bare land used for construction

	site	
	Industrial land	Land used for industrial purposes (e.g., wastewater treatment)

With the aid of a transformation matrix we described the conversion between land cover types quantitatively and reflected the dynamic of land cover change [55]. The results in a two-dimensional matrix highlighted the dominant change and the transition phases. One transformation matrix was calculated for each period for all land cover in the whole study area (all study sites were merged), resulting in a total number of six transformation matrices for active and former floodplains.

In recent years, landscape metrics have been an effective method to quantify the landscape pattern and the LULC change. The advantage of landscape metrics is their availability and comparability [56]. We calculated land cover configuration properties—shape, fragmentation and proximity—as well as composition characteristics—proportion, richness and evenness—for each period. To quantify the characteristics, we selected four indicators at the class level and four indicators at the landscape level (Table 2.3). The shape complexity of habitat and landscape indicates the amount of edge effects and undisturbed core area [57]. Landscape shape index (LSI) can assess the regularity of the landscape pattern [58]. It approximates one when the patch shapes are perfectly circular (vector format) or square (raster format) [59]. Fragmentation reflects the influences on the ecological communities attributed to human alteration of the landscape structure [60]. We used mean patch size (MPS) as a basic composition index [61] and effective mesh size (MESH) as a standard measure to quantify the fragmentation [62]. MESH characterizes the anthropogenic influences on landscapes from a geometric perspective. Proximity quantifies the habitat accessibility. Closer proximity reflects a more conductive configuration for the movement of the organisms and allows for more population exchanges [63,64]. Mean proximity index (PROX_MN) is inversely related to the nearest neighbor distance and it shows the non-isolation degree of patches. Landscape diversity describes the number and dominance of land cover types. The influence of landscape diversity on species diversity is complex, partly due to different species preferences to interior or edge of habitats [65,66]. Shannon's diversity index (SHDI) and evenness index (SHEI) are two popular metrics for the landscape analyses with emphasis on the richness and evenness of landscape composition [67].

Table 2.3 Landscape metrics calculated at landscape and class levels [56].

Abbreviation	Metrics	Description	Unit	Scale Level
LSI	Landscape Shape Index	Shape complexity of patches compared to standard shape	None	Landscape & class level
MPS	Mean Patch Size	Average patch size of each land cover	ha	Class level
MESH	Effective Mesh Size	Probability that two randomly chosen points of land cover located in the same patch	ha	Landscape & class level
PROX_MN	Mean Proximity Index	Proximity of all patches whose edges are within a specified search radius of the focal patch (in this study the radius is defined as 500 m)	None	Class level
SHDI	Shannon's Diversity Index	Diversity of land cover patches based on the number and distribution of patches	None	Landscape level
SHEI	Shannon's Evenness Index	Evenness of land cover patches based on the number and distribution of patches	None	Landscape level

The digitized maps were transformed into raster files with the cell size of 5 m × 5 m. This enabled us to calculate the landscape metrics with FRAGSTATS 4.2, to combine the maps with environmental data in raster format and to calculate the transition matrix. FRAGSTATS is a raster-based analysis program of spatial pattern to quantify the landscape pattern at patch, class and landscape scales [59].

We used the one-way analysis of variance (ANOVA) in R version 3.1.0 (R Core Team) to compare the changes of the structural metrics. The response variables are the landscape metrics, and the two factors are the floodplain type (active floodplain, former floodplain) and year (1963, 1978, 1995, 2010). To ensure the normal distribution of the residuals, we transformed some of the landscape metrics with log transformation, square-root transformation and power transformation.

2.2.3 Analysis of the relationship between land cover change and environmental factors

We used the Classification and Regression Tree Model (CART) to explore the relationship between environmental factors and land cover change. CART is a non-parametric method recursively partitioning the dataset of the response variable into homogeneous nodes, and the result is a decision tree [68]. All study sites were rasterized into pixels, and every pixel was characterized by environmental properties. Land cover change was the categorical response variable and environmental parameters were explanatory variables. We ran the CART model for each period of the land cover change of arable land (A), grassland (G), and riparian forest (R) both in active and former floodplains. All other forests and copse were summarized to group F, and all the other land cover types into group E (else). We selected fifteen types of land cover change from twenty-five possible changes based on the habitats of size importance (Table 2-A1). The CART model was calculated using the R package 'rpart' [69]. 'gini' was selected as the split index, the complexity parameter (CP) was set to 0.01, and the number of cross-validations was defined as 10. The CART model provides the relative variable importance (summing up to 100) to represent the variable influences.

Based on the review of existing studies, the main natural factors of land cover change are slope gradient, altitude, and soil characteristics [70,71]. Considering the dynamic characteristic of the floodplain, we expected that the topographic parameters (slope, aspect), the height above MW (mean water level), the distance to river and the soil parameters could be environmental factors related to the land cover change in this study. The study site was one variable for site differences. All the environmental factors were regarded as stable variables without temporal changes. Elevation, slope and aspect were extracted from the 10-m DEM. The MW data (provided by BfG) were given as height a.s.l. and represented the long-term mean water level of observation sites along the river. Height above MW was the difference between the absolute elevation a.s.l. and the mean annual water level. Distance to river was the distance from the pixel center to the center line of the river. The soil rating index and soil texture were derived from the German Soil Rating Survey (digital soil data was provided by LDBV). The soil rating index is an index with which soil productivity is rated by a single value between 0 and 100, originally surveyed for taxation purposes in Germany [72]. This index is only applied to agricultural land because it is an index evaluating agricultural productivity and is hence missing for forested land and the river. However, we kept the soil rating index in the correlation analysis because it is an important indicator of soil productivity and yield potential [73]. Besides that, the soil rating index correlates reasonably well with soil physical parameters including the clay content and the amount of organic substances [74]. The main soil textures in the study area are S (sand), Sl & lS (loamy sand), SL (very loamy sand), sL (sandy loam), L (loam) and MoL (moor/loam, soil consisting of peat and loam). Among the soil types in the study area, Leptosols and Regosols are formed on the more sandy soils, whereas Gleysols and Luvisols develop on the more loamy soils. Other soil parameters (e.g., organic matter, nutrient levels) could not be considered because these data are not available for the past. Soil texture and study site are categorical variables while all other variables are numeric. The CART method is robust to handle both variable types [68].

2.3 Results

2.3.1 Land cover change

The largest land cover type both in active and former floodplains is arable land (Fig. 2-A1). Although arable land in the active floodplain decreased during all periods, it still occupied the highest share (28.3%) in 2010. It was followed by grassland (15.6%), riparian forest (15.1%) and backwater (14.8%). Common characteristics of all land cover types in the active and the former floodplain are: Between 1963 and 2010 riparian forest increased while arable land and grassland declined. Grassland in the active floodplain decreased during all analyzed time spans. Grassland in the former floodplain decreased by 47%, and was therefore the land cover type with the strongest decline (Table 2.4). Built-up land and margin increased from 1963 to 1995 and then declined. Woody vegetation including riparian forest and other forest increased by 47% in the active floodplain and doubled in the former floodplain from 1963 to 2010. The area of riparian forest rose from 1963 to 1995, whereas in the last period it declined in most of the study sites (except Barbing).The percentage of agricultural land decreased from 1963 to 2010, while riparian forest increased.

Table 2.4 Net change of land cover in floodplain parts during all periods.

Land Cover	Active Floodplain			Former Floodplain		
Type	1963–1978	1978–1995	1995–2010	1963–1978	1978–1995	1995–2010
Riparian forest	4.01%	3.14%	−2.34%	0.07%	0.07%	0.48%
Forest	0.21%	0.03%	2.63%	0.00%	0.07%	0.67%
Copse	0.44%	−0.09%	0.11%	0.68%	1.02%	−0.41%

Arable land	−6.20%	−2.18%	−2.89%	0.92%	−1.42%	−0.50%
Grassland	−2.11%	−1.90%	−1.05%	−4.29%	−1.50%	−0.92%
Orchard	−0.06%	0.04%	−0.01%	−0.15%	−0.07%	0.13%
Artificial pond	−0.02%	0.02%	0.04%	0.85%	1.51%	0.42%
Backwater	4.00%	−0.46%	3.24%	0.04%	−0.01%	0.04%
Backwater lake	−0.45%	0.31%	0.16%	0.00%	0.03%	0.01%
Creek & Ditch	−0.03%	0.26%	−0.16%	0.00%	−0.05%	−0.02%
Field hedge/margin	0.31%	−0.16%	−0.09%	0.51%	−0.28%	0.05%
Road hedge/margin	−0.04%	0.74%	0.07%	0.56%	0.12%	0.05%
Vegetated path	0.01%	−0.38%	−0.01%	0.04%	0.13%	−0.39%
Path	0.14%	0.39%	−0.05%	0.22%	0.00%	0.16%
Road	0.01%	0.22%	−0.15%	0.48%	0.04%	0.03%
Settlements	0.01%	0.04%	0.08%	0.28%	0.20%	0.32%
Construction site *				−0.23%	0.10%	−0.14%

Note: * construction site only exists in the former floodplain.

In the active floodplain, all linear structures except field hedge increased from 1963 to 2010, while in the former floodplain, only road, path and margin increased. Path with vegetation experienced an obvious decline from 1978 to 1995, by contrast, paved path increased. The urbanized land cover—settlements, road and path—increased apparently in the former floodplain. There were relatively few roads in the study area, and their increase was accompanied with more road edges. Backwater in study site Barbing increased from 1963 to 1978 due to the creation of a backwater close to the river channel (Fig. 2-A1a). The increase of backwater from 1995 to 2010 in study site Gmünd resulted from the high water level and a small flooding event in 2010 (Fig. 2-A1b). Overall, the major changes in the active floodplain occurred in arable land, grassland, riparian forest and backwater. In contrast, in the former floodplain, built-up land experienced distinct increases.

The change maps in all study sites depict the overall trend in the land cover change between 1963 and 2010 (Fig. 2.3). The transformation matrix indicates the main changes between arable land, grassland and riparian forest (Table 2.5). One finding from the transformation matrix is that grassland in the active floodplain always changed into riparian forest or arable land.

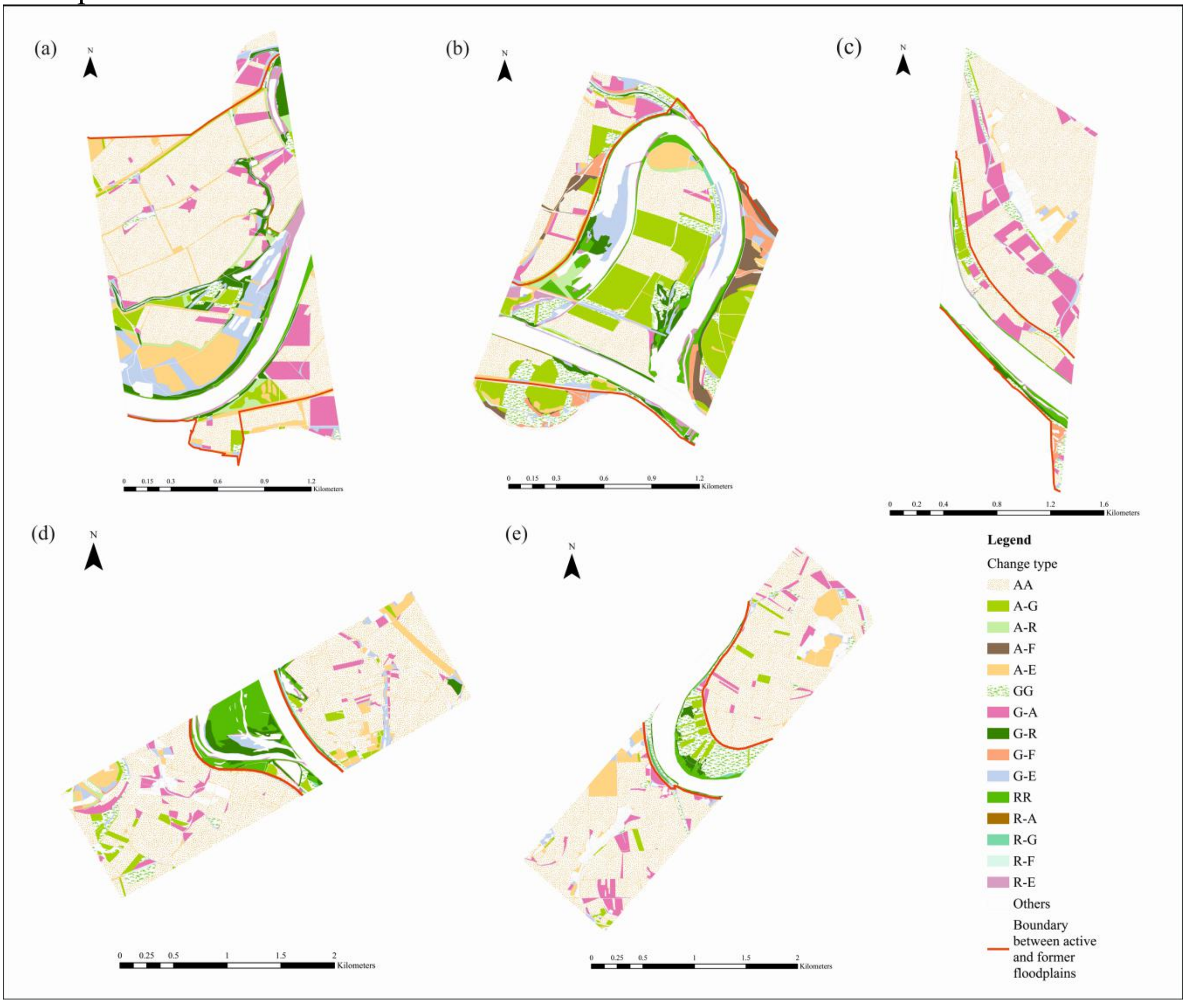

Fig. 2.3 Maps with changes of land cover in all study sites between 1963 and 2010. (a) Barbing; (b) Gmünd; (c) Irlbach; (d) Niederalteich; (e) Langkünzing. Abbreviation of change types please see Table 2-A1.

Table 2.5 Transformation matrix between land cover from 1963 to 2010.

	1963–1978		**1978–1995**		**1995–2010**	
Floodplain Type	**Land Cover Change**	**Changed Area (%)**	**Land Cover Change**	**Changed Area (%)**	**Land Cover Change**	**Changed Area (%)**
Active Floodplain	A-G	6.0	A-G	5.4	A-G	4.0
	G-A	3.4	G-A	4.8	G-A	1.4
	G-R	3.2	G-R	2.4	G-F	1.5
	total *	26.7	total	25.2	total	20.1
Former	A-G	4.0	A-G	3.7	A-G	2.6
	G-A	7.0	G-A	4.0	G-A	2.8

Floodplain	total	22.1	total	20.1	total	14.7

Note: A-G: Arable land to grassland; G-A: grassland to arable land; G-R: grassland to riparian forest; G-F: grassland to other forests. * The total change percentage is not the sum of the values in the table, but it also includes those changes lower than 1%, which are not shown here.

The area of grassland changing to riparian forest and the area of arable land transforming into grassland decreased during all the periods. In contrast, in the former floodplain, the conversion between arable land and grassland decreased (Table 2.5). The transformation percentage of grassland to arable land in the active floodplain increased in the second period and then decreased.

2.3.2 Structural change of land cover

2.3.2.1 Landscape level

In the ANOVA of the landscape metrics, some metrics differ significantly between the active and former floodplain (Table 2.6). The fragmentation of arable land changed significantly over time (Table 2.6). Although the structural metrics of riparian forest and grassland did not change significantly in the overall area, the changes occurring in some of the study sites are obvious. In the active floodplain, the shape complexity of the landscape was reduced from 1963 to 1978, it stagnated in the second period, and then the reduction continued from 1995 to 2010 (Table 2.6). In the active and former floodplain parts the landscape experienced a fragmentation from 1963 to 1995 in Barbing and Gmünd (Fig. 2-A1a,b). Although fragmentation decreased in recent years, the landscape in the former floodplain in Barbing, Gmünd, Irlbach and Niederalteich (Fig. 2-A1a–d) was still more fragmented in 2010 than in 1963. The diversity of land cover in the active and former floodplain in Barbing and Gmünd increased (Table 2.6). Landscape shape in the former floodplain in Barbing, Gmünd and Irlbach (Fig. 2-A1a–c) became more complex in early periods but then the shape complexity decreased slightly from 1995 to 2010.

Table 2.6 Mean values of structural metrics: landscape, arable land, grassland and riparian forest in active and former floodplains from 1963 to 2010.

Landscape Metrics	**Active Floodplain**				**Former Floodplain**			
	1963	**1978**	**1995**	**2010**	**1963**	**1978**	**1995**	**2010**
Landscape								
LSI	11.06 ± 0.80	10.62 ± 1.01	10.84 ± 1.22	9.96 ± 1.34	11.45 ± 2.24	12.05 ± 2.27	12.91 ± 1.63	12.48 ± 1.57
MESH (ha)	20.14 ± 7.17	18.88 ± 6.69	13.70 ± 2.27	18.50 ± 2.52	33.68 ± 10.68	30.76 ± 11.55	28.48 ± 14.16	26.93 ± 11.16
SHDI **	1.26 ± 0.09	1.33 ± 0.08	1.29 ± 0.11	1.30 ± 0.13	0.95 ± 0.02	0.98 ± 0.06	1.15 ± 0.08	1.17 ± 0.12
SHEI ***	0.51 ± 0.04	0.53 ± 0.03	0.51 ± 0.02	0.54 ± 0.04	0.37 ± 0.02	0.37 ± 0.02	0.42 ± 0.03	0.43 ± 0.04
Riparian forest								
LSI ***	10.4 ± 1.65	11.04 ± 1.50	10.92 ± 1.60	10.12 ± 1.81	3.40 ± 1.53	3.67 ± 1.50	5.51 ± 1.58	4.54 ± 1.36
MPS (ha) ***	1.21 ± 0.14	1.91 ± 0.35	2.21 ± 0.51	1.92 ± 0.27	0.13 ± 0.08	0.37 ± 0.16	0.29 ± 0.11	0.38 ± 0.23
MESH (ha) ***	1.38 ± 0.72	2.76 ± 1.52	3.40 ± 1.57	4.38 ± 3.04	0.004 ± 0.004	0.005 ± 0.003	0.008 ± 0.003	0.018 ± 0.013
PROX_MN ***	92.76 ± 28.17	192.92 ± 61.95	475.44 ± 184.33	131.04 ± 35.44	4.02 ± 2.57	3.84 ± 3.38	12.61 ± 5.13	1.78 ± 2.86
Grassland								
LSI	10.16 ± 1.04	8.37 ± 0.93	8.76 ± 1.28	7.84 ± 0.92	10.24 ± 2.29	9.40 ± 1.76	8.95 ± 1.45	8.34 ± 1.48
MPS (ha) *	0.61 ± 0.08	0.63 ± 0.16	0.66 ± 0.09	0.87 ± 0.12	0.48 ± 0.04	0.50 ± 0.06	0.53 ± 0.15	0.50 ± 0.14
MESH (ha) *	4.71 ± 2.51	3.70 ± 2.06	3.98 ± 2.88	4.82 ± 2.95	1.10 ± 0.37	0.60 ± 0.32	0.55 ± 0.33	0.53 ± 0.37
PROX_MN	260.80 ±	190.80 ±	140.19 ±	146.77 ±	143.39 ±	59.90 ± 20.29	68.57 ± 35.09	54.17 ± 28.68

	135.28	81.88	54.21	86.10	51.05			
Arable land								
LSI **	5.61 ± 0.34	5.16 ± 0.65	4.18 ± 0.88	3.56 ± 0.71	7.83 ± 1.69	7.54 ± 1.59	7.49 ± 1.33	7.06 ± 1.40
MPS (ha)	0.53 ± 0.14 ^{a}	0.55 ± 0.15 ^{a}	1.08 ± 0.25 ^{ab}	1.42 ± 0.33 ^{b}	0.43 ± 0.06 ^{a}	0.15 ± 0.07 ^{ab}	1.19 ± 0.06 ^{ab}	1.39 ± 0.05 ^{b}
MESH (ha) ***	12.09 ± 7.92	10.47 ± 7.47	4.01 ± 1.93	4.73 ± 2.85	32.51 ± 10.96	29.94 ± 11.69	27.76 ± 14.24	26.18 ± 11.27
PROX_MN **	326.47 ± 182.93	626.89 ± 396.60	312.33 ± 250.61	347.65 ± 304.18	2111.83 ± 838.54	2269.85 ± 896.74	1982.81 ± 798.20	2874.85 ± 1102.47

Note: Mean ± SE; Abbreviations: LSI = landscape shape index; MPS = mean patch size; MESH = effective mesh size; PROX_MN = mean proximity index; SHDI = Shannon’s diversity index; SHEI = Shannon’s evenness index. Signif. Codes within factor “floodplain type”: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1. Letters “^{a}” “^{b}” “^{ab}”: significant groups ($p < 0.1$) within factor “Year”.

2.3.2.2 Class level

The patches of the class level 'arable land' had a more regular shape in the active floodplain in Barbing, Irlbach, Langkünzing (Fig. 2-A1a,c,e). Arable land had a more complex shape in the former than in the active floodplain, but the shape complexity decreased with time in Gmünd and Niederalteich (Table 2.6, Fig. 2-A1b,d). The change of MESH showed a strong fragmentation of arable land in Barbing, Gmünd, Niederalteich and Langkünzing (Fig. 2-A1a,b,d,e) from 1978 to 1995, but then this trend was reduced. Compared to the situation in 1963, arable land in the floodplains in Barbing, Gmünd and Niederalteich (Fig. 2-A1a,b,d) became more fragmented in 2010. The patches of arable land in the active and former floodplain in all study sites became significantly larger all the time (Fig. 2-A1, Table 2-A2). The patches were closer to each other in the former floodplain in Barbing, Irlbach and Langkünzing in the first period, but from the 1970s to the 1990s this trend was reversed, and afterwards the proximity continued to increase.

The shape complexity of grassland decreased in the active floodplain and grassland patches in the active floodplain in Barbing, Gmünd, Irlbach and Langkünzing (Fig. 2-A1a–c,e) became larger. The grassland structure was more fragmented in Barbing, Niederalteich and Langkünzing (Fig. 2-A1a,d,e) from 1963 to 1978, but in the next periods it recovered gradually (Table 2.6). The grassland patches of the former floodplain in Irlbach, Niederalteich and Langkünzing (Fig. 2-A1c–e) became more regular in shape. They had no obvious change in average size but became organized. Grassland in the former floodplain in Barbing, Gmünd, Irlbach, Langkünzing experienced a fragmentation, and the patches in Barbing, Irlbach, Niederalteich and Langkünzing diverged more from each other than in 1963 (Table 2.6).

The shape complexity of riparian forest in the active floodplain in Irlbach and Niederalteich (Fig. 2-A1c,d) declined continuously. The patches in Gmünd, Niederalteich and Langkünzing (Fig. 2-A1b,d,e) became larger at first, but later slightly smaller (Table 2.6). In the active floodplain riparian forest tended toward a more aggregated structure in all study sites from 1978 to 1995 and it continued in Barbing, Irlbach and Niederalteich after 1995. The proximity of patches in Gmünd and Niederalteich (Fig. 2-A1b,d) was enhanced from 1963 to 1995, in the last period it went through a fall, but the final proximity was higher than that in 1963. The patch size of the riparian forest (in the former floodplain this refers to forests close to water bodies) was larger in the first period, and then with a small fluctuation it was larger in 2010 than the starting state in Barbing, Gmünd and Niederalteich (Fig. 2-A1a,b,d).

2.3.3 Relationship between the change of land cover and environmental factors

To have an intuitive impression of the relationship between the environmental factors and the land cover changes, we show the CART results of riparian forest and grassland from 1963 to 1978 exemplarily (Fig. 2.4 and Fig. 2.5). Most riparian forest in the active floodplain of study sites Irlbach, Niederalteich and Langkünzing stayed stable from 1963 to 1978 (Fig. 2.4). In study sites Barbing and Gmünd, riparian forest located higher than about 1 m below MW remained stable. Among the riparian forest lower than 1 m below MW, those forests with a northeast orientation and further than approximately 500 m to the river were converted to grassland; the rest did not change.

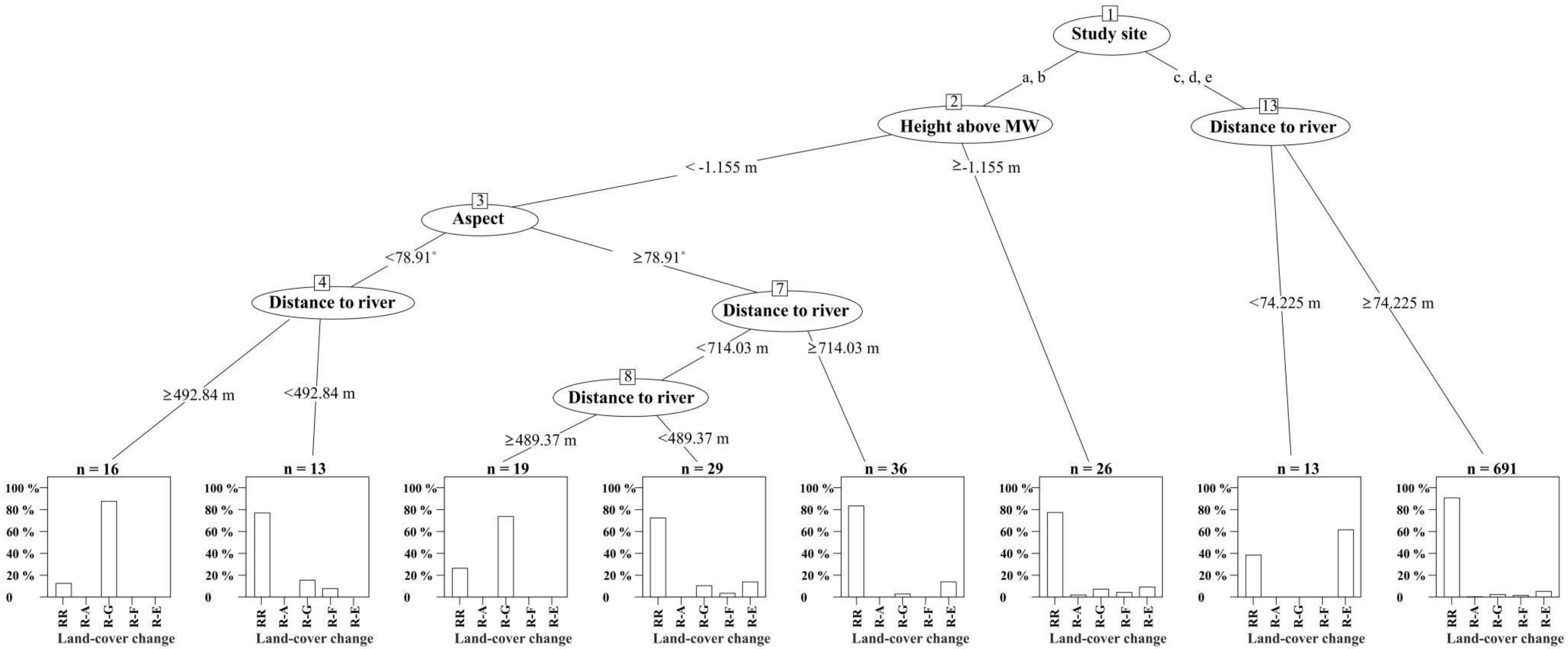

Fig. 2.4 The CART result of riparian forest change and environmental factors from 1963 to 1978. Abbreviations: RR: stable riparian forest; R-A: riparian forest to arable land; R-G: riparian forest to grassland; R-F: riparian forest to other forests; R-E: riparian forest to other land cover; the small letters refer to the study sites, see Fig. 2.1.

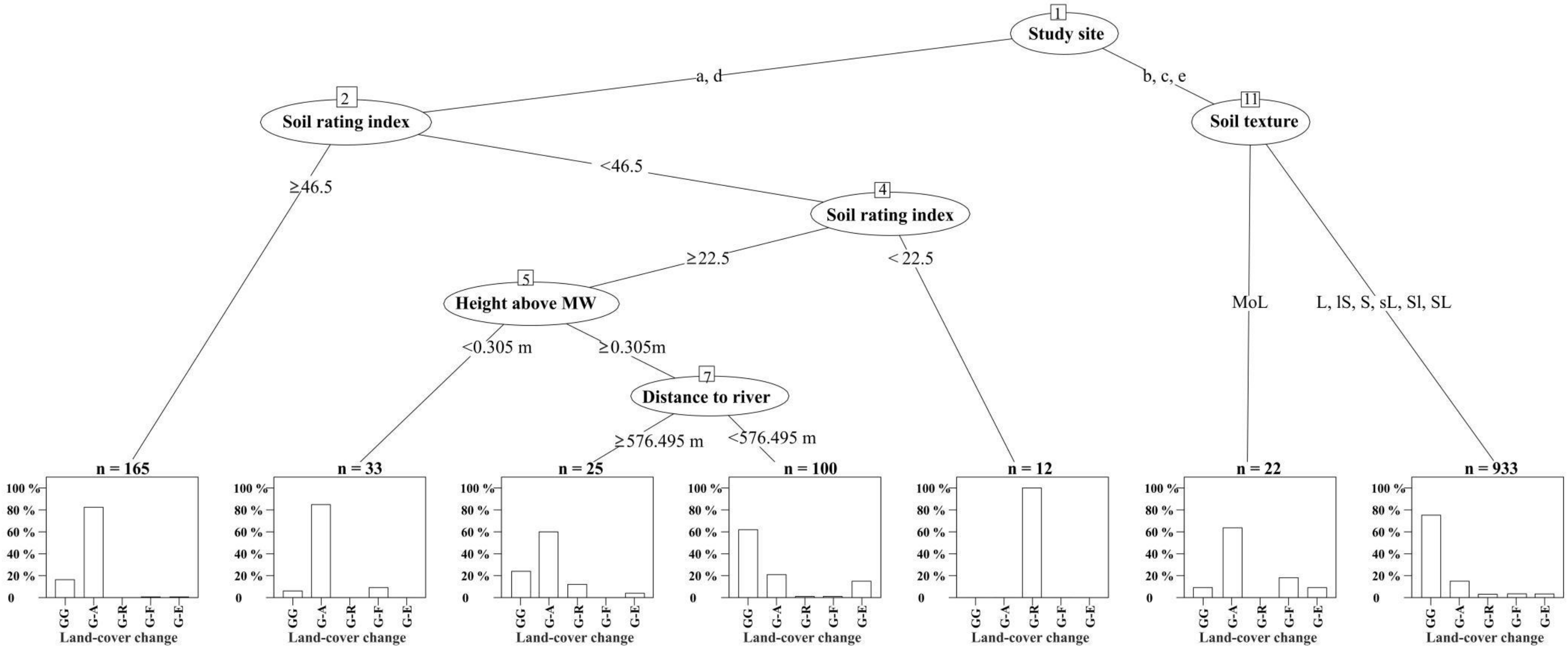

Fig. 2.5 The CART result of grassland change and environmental factors from 1963 to 1978. Abbreviations: GG: stable grassland; G-A: grassland to arable land; G-R: grassland to riparian forest; G-F: grassland to other forests; G-E: grassland to other land cover; S: sand; Sl & lS: loamy sand; SL: very loamy sand; sL: sandy loam; L: loam; MoL: moor/loam, soil consisting of peat and loam; the small letters refer to the study sites, see Fig. 2.1.

In the active floodplain of study sites Gmünd, Irlbach and Langkünzig, most grassland stayed stable from 1963 to 1978 and only a small proportion of grassland with soil consisting of peat and loam converted into arable land (Fig. 2.5). In the active floodplain of study sites Barbing and Niederalteich, grassland with higher soil rating indexes changed into arable land; grassland with lower soil rating indexes became riparian forest; grassland with medium soil rating indexes and closer to the river persisted. As expected, patches farther away from the river are more likely to change into arable land.

In this study, elevation and distance to river were the most important environmental factors to land cover change in the floodplain. The most relevant environmental factors for arable land and grassland changes are soil rating index, height above MW and distance to river; for riparian forest and other woodland, the most important factors are height above MW and distance to river (Table 2.7). The high values for 'study site' showed different trends between study sites (see Fig. 2-A3 to Fig. 2-A5).

Table 2.7 The relative importance of environmental factors to land cover change.

Environmental Factors	**Arable Land Change**			**Grassland Change**			**Riparian Forest Change**		
	1963 –1978	**1978 –1995**	**1995 –2010**	**1963 –1978**	**1978 –1995**	**1995 –2010**	**1963 –1978**	**1978 –1995**	**1995 –2010**
Aspect	2	1	2	1	1	5	10	11	8
Distance to river	15	14	22	4	13	31	43	7	26
Height above MW	10	22	22	18	21	18	20	46	26
Slope	4	4	4	2	2	5	9	2	5
Soil rating index	42	18	16	18	13	26			
Soil texture	7	18	16	26	9	10			
Study site	20	23	18	31	41	6	17	34	34

Note: Results were calculated with CART, and the relative importance to each land cover change type during one period sums up to 100.

2.4 Discussion

2.4.1 How did the floodplain land cover change?

The increasing patch size of agricultural land in this study is consistent with comparative studies in Germany, in which many small grassland patches were merged after 1953 [75]. It reflects agricultural intensification with new technical and production methods. Meeus [76] and Hietel et al. [70] showed the trend in agriculture to either intensification or abandonment. While less productive agricultural areas got abandoned, fertile areas were used more intensively. This process started in the 1970s by the Land Consolidation Act in Germany to enhance the agricultural efficiency and reduce the fragmentation with redistribution of small non-adjacent fields between farmers. This action lowered agricultural land division and enlarged the farm size [77]. The observed increase of riparian forest especially close to the river and in low heights above MW indicated that agricultural land use near the river became de-intensified, because high water levels threaten the field cultivation.

The core area and proportion of agricultural land decreased in the active and the former floodplain. In general, the loss of agricultural land could be explained by the German agricultural policy. Since 1962, German agriculture has been under the instruction of EU's Common Agriculture Policy (CAP) to provide affordable food and to improve the living standard of the farmers [78]. The CAP has contributed to the large-scale land cover change in the past decades [79]. Land cover change in this study was partly related to this development. To enhance the production level was the main focus of the CAP until 1984. Then the measures were adjusted because of the excessive production (e.g., dairy products) above the market demand. After 1992, the farmers were supported with direct aid payments to work more environmentally friendly [80]. Since 2003, with more emphasis on biodiversity conservation, water management and soil protection, the CAP has provided the farmers with income support and motivated them to adopt sustainable agricultural practices [79]. From 2007 to 2013, the Bavarian Cultural Landscape Program (KULAP) provided the farmers with subsidies for the afforestation on agricultural land [81]. In this study, despite the high soil fertility, part of the agricultural land was transformed into riparian forest due to the unreliable water conditions in the floodplain. Nevertheless, the agricultural land still maintained a high share in the active floodplain, which is ecologically negative for the floodplain [82].

Besides the specific land cover change, the floodplain landscape in some study sites experienced a strong fragmentation despite the slight improvement in the active floodplain after 1995. It was shown that the increasing landscape fragmentation in Central Europe was a consequence of patchwork conversion, site development, increasing infrastructure land [62] and water engineering [83]. In this study, the increase of linear structures (road and path) contributed to the increase of shape complexity and landscape fragmentation. The transportation lines can interrupt the natural disturbance regime and lead to the degradation of floodplain habitats, as was found by Blanton and Marcus [84].

2.4.2 Did the grassland in the study area decrease?

The area of grassland decreased continuously during the last decades, because grassland was transformed into arable land and riparian forest. Species-rich meadows along the Upper Rhine River have been transformed into arable land since the Middle Ages [85]. The transformation of permanent grassland into arable land due to land-use intensification was also a contributor to the decrease of grassland in the studies by Walz [75] and Tscharntke et al. [86]. Besides land-use intensification, the CAP also stimulated the loss of grassland (see Section 2.4.1).

Given the importance of grassland in ruminant livestock production, grassland change was partly in line with the variation of livestock number, as discussed by Chang et al. [87] in their work on grassland productivity and ruminant livestock density in Europe. The agricultural statistics in all municipalities within the study area (Fig. 2-A2) provided by the Bavarian State Office for Statistics (LfStat) showed an increasing cattle number from 1963 to 1978 and a decrease from 1978 to 2010. Up to 1970 cattle stayed in summer on pastures and were additionally fed with grass and in winter with hay (additional mash), which caused high grass consumption. From 1970 green maize (silage) became the important forage and the demand for arable fields rather than grassland increased. Since the 1980s, dairy products have been reduced, and the cattle number decreased. The decline of livestock production and a preference for market crop production contributed to the transformation from grassland to arable land. As a consequence, the agricultural intensification weakened the grassland demand [7].

Habitat loss and fragmentation reduce the grassland connectivity. The change of connectivity is a crucial aspect of land cover change and implies the spatial alteration of habitat continuity [88]. In this study, the decrease of proximity between grassland patches in most study sites implicates the loss of connectivity. Besides that, margins such as ‘field margin’ and ‘path with vegetation’ were gone, together with their ecological functions, e.g., as migration corridor and for biodiversity enhancement.

2.4.3 Did the riparian forest in the study area decrease?

Although the riparian forest decreased overall in the time span between 1995 and 2010, the total area of riparian forest increased up to now. Riparian forest change varies worldwide. Due to hydroelectric power stations and other management measures, the Rhine Alsatian forest and the Austrian forest along the Danube River decreased by 25–50% from the 1930s to 1980s [82]. The cumulative loss of riparian forest was driven by dam construction, intensive agriculture (enhancement of maize production on former grassland sites), urban development, forest management and timber harvesting [83]. In our study region, the river engineering projects between Straubing and Vilshofen from the 1990s had strong influences on the floodplain habitats. The flood protection measures led to the change of site parameters including depth to groundwater level, groundwater fluctuations and flow rate. They further resulted in a loss of area for natural development. Some parts of the forested area in the floodplain shifted to the water zone or even open water area [89].

The main increase of riparian forest area in this study originated from the transformation from grassland and arable land. This could be explained by land-use policy change in Western Europe (foundation of EWG in 1957, EU in 1993). The CAP supported the afforestation of agricultural land, and this gave rise to an increase of 4.9% forest in the Federal Republic of Germany from 1950 to 1993 [90]. This afforestation compensated clear cuttings and led to an increase of the forest cover [91]. In this study, riparian forest in most study sites became more aggregated in the last 50 years. Forest patches grew larger from 1963 to 1995 in the active floodplain, and the patch shape was more regular than before. In contrast, floodplain forests along other large rivers (e.g., the Upper Rhine River) have experienced strong fragmentation in the last decades [82].

In German floodplain management practices, to ensure the flood retention, riparian forest was removed to decrease the roughness and increase the water velocity. Since 2004, management measures including the thinning of softwood stocks have been taken in the Danube Waterway Project between Straubing and Vilshofen [92]. However, in forest restoration projects along the Middle Elbe River, it was shown that forest plantings in suitable positions can help to control flooding. Due to the increased roughness in the planted forests, water is kept in areas designated for flood retention. Flood waves are flattened and flood-sensitive areas are secured. This form of landscape management is a solution for the conflicts between natural conservation and flood protection [22], but due to the high population density and limited amount of space along the Upper Danube River, this measure is probably not suitable in our study area.

2.4.4 Suitability of landscape structure analysis

Landscape metrics were used to analyze the land cover pattern and to quantify the fragmentation. As a prerequisite to the study of landscape function and change, much effort has been put into calculating the landscape metrics to quantify the landscape structure in previous studies [93]. However, these metrics have to be selected and interpreted in relation to their ecological meaning [94]. Without supporting data on species level, only general landscape patterns and processes can be pointed out.

We selected the landscape metrics in consideration of their ecological meanings. Effective mesh size (MESH) and edge density are measures to quantify the fragmentation, which affects processes like animal dispersion and habitat viability [95]. The increase of MESH indicated the more aggregated structure of riparian forest, which benefits the species that are sensitive to edge effects [57]. The shape index indicating the shape complexity of the forest affects the bird abundance [57]. The shape of habitat fragments also influences animal population dynamics and meta-population persistence within fragments [96].

Even though it is not possible to draw conclusions on specific ecological processes or the effects of changes on single species groups [93], the analysis of landscape metrics gives information about the changes in landscape structure and landscape structural composition over time and the general effects of these changes. Suitable landscape metrics that are easy to interpret by stakeholders and decision-makers who are responsible for planning and management can help to increase the understanding for landscape structural and functional patterns.

2.4.5 Relationship between grassland and riparian forest change and environmental factors

For the agricultural land cover change, soil quality played the most important role. The importance of the variable 'study site' implied different changes between study sites. Previous researchers found that land cover changes in submontane landscapes of Germany were correlated with physical landscape attributes, e.g., elevation, slope, aspect, water capacity and soil texture [70,97]. Other studies reported the importance of relief, hydrological and soil conditions in the active floodplain: the principal environmental gradients: hydroperiod, the depth of the groundwater table and soil fertility determine water → plant → soil interactions [98]. Height above MW is related to hydrological differences. Higher sites in the floodplain are much drier than lower sites because they are farther from the groundwater table. Distance to river is a significant factor for the spatial variability in the depth and duration of inundation, soil properties, nutrient accumulation and other ecological processes in the floodplain [99]. Bürgi and Turner [100] detected different land cover changes in various soil conditions: agricultural land changed into forest as a result of agricultural abandonment on shallow soils; arable land changed into grassland due to the decline of farming intensity on more sandy and deeper soils; fertile grassland sites on silty soils were transformed into arable land owing to agricultural intensification. Along many European rivers, the original floodplain forests were cleared for agricultural production on fertile soils [82]. In the present study, grassland in the active floodplain with higher soil rating indexes changed into arable land, while grassland with lower soil rating indexes tended to change into riparian forest, which confirmed less preference of agricultural production on these soils. The farmers tend to convert the grassland with higher productivity into arable land to improve the agricultural production. In this study riparian forest change was mainly related with height above MW and distance to river. The flood-dependent attributes and the preference for high groundwater level of riparian forest allowed these sites to develop into forest [2].

2.4.6 What is the ecological relevance of the observed trends in the floodplain?

The decline of agricultural land and the increase of riparian forest compared to the original state positively affect the floodplain. As a natural habitat, riparian forest is of high importance in river-floodplain ecosystems. It can reduce the sediment amount in the river and help to mitigate the flood risk [101]. The clearance of riparian forest for overflow optimization is caused by human population's demand for safe living conditions, but it should be in harmony with the protection of flora and fauna. The hydraulic roughness of floodplain vegetation could be modeled to see the influences on flood water level and to reinforce coordination between ecosystem rehabilitation and flood safety [102].

On the landscape level, the finding of increasing fragmentation in the floodplain is a warning signal for the loss of biological diversity and ecological functions [103]. In other studies, poor connectivity and strong fragmentation of floodplain result in a lower rate of mineral sedimentation and P accumulation [104]. In this study agricultural intensification shifted the arable land into larger fields, which equalized the conditions and had negative impacts on species diversity, as also found by Harms et al. [105]. Fertilizers and pesticides used in agriculture can lead to groundwater pollution and river eutrophication. The natural forests in floodplains should be protected to provide refuges for species and to improve biodiversity generally [83].

2.5 Conclusions

In the Upper Danube Floodplain, our study focused on the change of land cover and the relevant environmental factors. The increasing fragmentation of the floodplain landscape was a consequence of the disturbance by water management, agricultural intensification and linear infrastructure. In spite of the decline of agricultural land in the floodplain in recent decades, it still accounted for a large proportion in the active floodplain and agricultural intensification threatened the ecological functions of floodplain habitats. The aggregated structure of riparian forest is likely to have positive influences from an ecological view. However, the trend of increasing riparian forest was relativized by cutting forests for flood protection, Given that the Danube is an important federal waterway, the local water management office made plans to protect the riparian forest and limit the intensive agricultural use in the Danube Floodplain [106]. To achieve a sustainable floodplain development, an agreement between different interests, e.g., shipping traffic, flood protection and nature conservation has to be reached.

Acknowledgments: We would like to thank The German Federal Institute of Hydrology (BfG), the Bavarian State Office for Survey and Geoinformation (LDBV), the Bavarian Environment Agency (LfU) and the Bavarian State Office for Statistics (LfStat) for the provision of data. We are thankful to all colleagues from the Division of Landscape Ecology and Landscape Planning for suggestions and discussion in the research process. This study is funded by a Ph.D. scholarship to Fang Xu awarded by the China Scholarship Council (CSC) and we appreciate the financial support.

Author Contributions: Conceived and designed this study: Fang Xu, Annette Otte, Kristin Ludewig, Tobias W. Donath, Sarah Harvolk-Schöning; Analyzed the data: Fang Xu; Wrote the paper: Fang Xu; Revised the paper: Annette Otte, Kristin Ludewig, Tobias W. Donath and Sarah Harvolk-Schöning. All authors read and approved the final manuscript.

Conflicts of Interest: The authors declare no conflict of interest. The founding sponsors had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, and in the decision to publish the results.

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3. Factors determining the distribution pattern of floodplain vegetation remnants along the Danube River between Straubing and Vilshofen

Welche Faktoren bestimmen die Verteilungsmuster von Restbeständen der Auenvegetation an der Donau zwischen Straubing und Vilshofen?

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Keywords: hydrological alteration, landscape fragmentation, agricultural activities, plant species composition, riparian habitats

Abstract

Floodplains are of high importance for biodiversity and ecological functions due to their spatio-temporal heterogeneity. To understand the human influences on the floodplain vegetation, we analyzed 108 vegetation relevés in the Danube Floodplain in Germany. Ten vegetation types (e.g., floodplain meadows, river bank vegetation, softwood forests, hardwood forests) were identified among the woody and open land vegetation. They reflected the hydrological gradient in the floodplain. We explored the relationship between the species composition and environmental variables from the landscape level to the local level using Non-Metric Multidimensional Scaling (NMDS), Boosted Regression Trees (BRT), and Classification and Regression Trees (CART). Even in a floodplain that is heavily influenced and altered by humans, such as the study area, the hydrological regime was still the most important factor determining species composition. Furthermore, the landscape fragmentation and the land use (e.g., agriculture) also played an essential role. Although the composition of vegetation types along the Danube Floodplain is similar to floodplain vegetation under natural conditions, some groups lost their original habitats (e.g., softwood remnants) due to the landscape fragmentation caused by infrastructure or they occurred in atypical habitats. For instance, the short-lived species that typically occur at the river banks were confined to the banks of backwaters and gravel lakes due to the regulation of the main river channel. Therefore, factors at all levels need to be taken into consideration before starting a planning process in floodplains.

Erweiterte deutsche Zusammenfassung am Ende des Artikels

3.1 Introduction

Floodplains are characterized by a high diversity of habitats and biota as a result of spatial and temporal heterogeneity (NAIMAN et al. 1993, WARD et al. 2002, H RDTLE et al. 2006). Vegetation in the floodplain is affected by abiotic (e.g., flooding events) and biotic factors (e.g., the life cycle of species, M LLER 1995). RONGOEI et al. (2014) identified the hydrological regimes (e.g., the surface- and ground-water regime, bedload, and nutrient load) and agricultural activities (e.g., crop cultivation) as the main factors driving species composition in a floodplain. In Central Europe, the floodplains have suffered a massive loss of species diversity as the result of human interference (SCHNEIDER 2010). Human impacts on the floodplain include agricultural activities, nutrient input in the river, and civil engineering measures (e.g., river regulations, hydroelectric power plants). The anthropogenic activities, such as agricultural production, river regulations, and bank fixation, alter the hydrological conditions, including runoff patterns, inundation regimes, erosion rates, and sediment load (HAMILTON 2002). Agricultural intensification and increased nutrient input cause severe species loss in the floodplain grasslands in Northern Germany (WESCHE et al. 2012). Additionally, many natural floodplain communities, such as floodplain forests, have been replaced by agricultural land (OPPERMAN et al. 2010). These land-cover changes also induce structural landscape changes. For instance, the previously continuous forests are now fragmented, due to agricultural production and infrastructure construction (BLANTON & MARCUS 2009).

Landscape fragmentation affects the recruitment in riparian forests and results in a loss of biodiversity in these habitats (HANSON et al. 1990). Disruption to the forest borders (e.g., hardwood floodplain forest) threatens the natural species composition (PETR ŠOV -ŠIB KOV et al. 2017). Edges created by the adjacent environment (e.g., settlements, agriculture) cause changes in abiotic and biotic gradients, and lead to responses of the forest structure and species composition (HARPER et al. 2005). Human impacts on species diversity can be measured by applying the concept of landscape hemeroby (SUKOPP 2004): low to moderate human impacts promote species richness, while strong human impacts reduce species diversity (WALZ & STEIN 2014). The common species displace the rare species, as a result of the increasing human impacts (KOWARIK 1988).

Natural and human disturbances affect the floristic composition and vegetation structure in floodplain habitats, such as forests and grasslands (BANASOVA et al. 2004). Forests form the natural vegetation in floodplains, and their species composition strongly depends on environmental gradients and riparian processes (TABACCHI et al. 1996). In Central Europe, floodplain forests have disappeared or have been reduced, due to river management, and they are a threatened habitat (HUGHES 1997).

In floodplains under agricultural use, floodplain forests are replaced mainly by grassland. Due to traditionally low management intensity and strong hydrological dynamics, floodplain grasslands host high species diversity and many endangered species (LUDEWIG et al. 2014). Some floodplain grasslands are protected by the European Union's Habitats Directive (e.g., floodplain meadows of the *Cnidion dubii*, Council Directive 92/43/EEC, habitat type 6440). Since the 1950s, degradation and loss of European floodplain grasslands have occurred due to agricultural intensification, e.g., drainage, inorganic fertilization, and transformation to arable land (KRAUSE et al. 2011).

Natural floodplains are composed of habitats organized by physical disturbances (Müller 1995). In floodplains experiencing strong human disturbances (e.g., channelization, river regulation), the species diversity is reduced and the habitats of plant communities changed (NILSSON & JANSSON 1995, M LLER 1998). Most studies explored the relationship between species composition and environmental factors in floodplains either at the landscape or local level (e.g., site gradients like soil fertility, soil moisture and soil chemistry-related variables, H RDTLE et al. 2006, SLEZ K et al. 2017). Single measures at the landscape level (e.g., edge density) were included in the explanation of floristic gradients (M NDEZ-TORIBIO et al. 2014). However, a systematic investigation of structural landscape parameters was rarely included, even though the landscape pattern may be important to species establishment and distribution. To understand the human influence on vegetation patterns, we analyzed the relationship between environmental variables (abiotic and landscape factors) and species composition along the Upper Danube from the landscape to local level. The following research questions were addressed:

- How are plant species composition, landscape pattern, and environmental variables related in the Danube Floodplain?
  - How are the hydrological parameters related to species composition?
  - How are the landscape structural parameters related to species composition?
  - How are the site-specific parameters related to species composition?
- In floodplains under strong human influences, where are the habitats for vegetation types located?

3.2 Material and Methods

3.2.1 Study area

The study area is located along the Upper Danube River in Bavaria, Southern Germany (River-km 2,319–2,255; Fig. 3.1). The Danube River is an international waterway, which originates in the Black Forest in Germany and flows into the Black Sea with a pluvial-nival flow regime. As an essential bio-corridor in Europe and a hotspot of natural habitats, the Danube River is of high natural value. The Upper Danube refers to the part of the river that runs from its source to the confluence with the Morava River (River-km 2,415–1,791). It runs for 587 km through Southern Germany, and this section of the river is characterized as mountainous with low water temperature and high flow velocity. In this study, we analyzed the species composition along the Upper Danube between Straubing and Vilshofen. This part of the floodplain hosts many endangered species, and it is one of the very few free-flowing stretches, as the Upper Danube is interrupted by 59 dams along the first 1,000 kilometers (HEIN et al. 2016). Soils in the Danube Floodplain are heterogeneous with various grain sizes and textures (HAGER & SCHUME 2001). The predominant soil types are gleysols, fluvisols, cambisols, and luvisols (digital soil data provided by the Bavarian State Office for Survey and Geoinformation, LDBV). The study area has a temperate climate with a mean annual temperature of 8°C and a mean annual precipitation of 656 mm (mean value from 1981 to 2010 for climate station Straubing, German Meteorological Service (DWD) 2013).

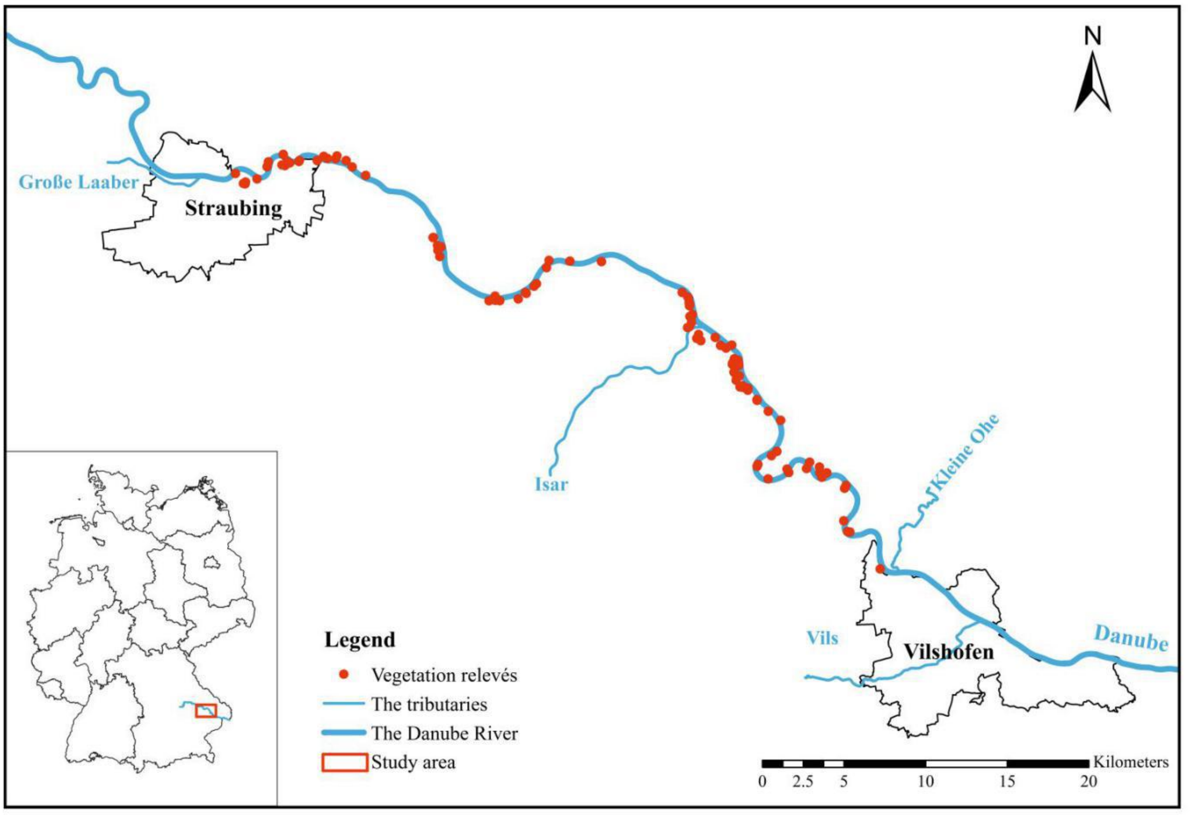


Fig. 3.1 Locations of vegetation relevés between Straubing and Vilshofen along the Upper Danube. Source: Germany map: VG250 (Administrative boundaries 1: 250,000), provided by the Federal Agency for Cartography and Geodesy (BKG 2007); Vegetation relevés: data collected in the context of "Variantenunabhängige Untersuchungen zum Ausbau der Donau zwischen Straubing und Vilshofen" by the German Waterways and Shipping Administration (BfG 2013); the shapefile of the Danube was provided by BfG; the tributaries were manually digitalized based on the Bing Maps Aerial in 2012 (30 cm resolution; © 2012 Microsoft Corporation).

Abb. 3.1 Standorte der Vegetationsaufnahmen zwischen Straubing und Vilshofen entlang der Oberen Donau. Quelle: Deutschlandkarte: VG250 (Verwaltungsgrenzen 1: 250.000), erstellt vom Bundesamt für Kartographie und Geodäsie (BKG 2007); Vegetationsaufnahmen: Daten, die im Rahmen der "Variantenunabhängigen Untersuchungen zum Ausbau der Donau zwischen Straubing und Vilshofen" von der Bundesanstalt für Gewässerkunde (BfG 2013) erhoben wurden; Verlauf der Donau zur Verfügung gestellt von der BfG; Die Nebenflüsse wurden auf Basis der Bing Maps Aerial in 2012 manuell digitalisiert (30 cm Auflösung; © 2012 Microsoft Corporation).

The Potential Natural Vegetation (PNV) in the study area is alluvial hardwood forest with *Fraxinus excelsior* and *Ulmus minor* in complex with softwood forest elements (e.g., *Salix* *alba*). The softwood forest would occur close to the river, where the main soils are gleysols, fluvisols, or cambisols (digital soil data provided by the LDBV). In the higher areas and on consolidated terraces of the floodplain with luvisols or cambisols on the loess loam sediments, the PNV is alluvial hardwood forest of *Ulmus minor*, *Fraxinus excelsior*, and *Carpinus betulus* (SUCK & BUSHART 2012a, 2012b).

The Danube Floodplain consists of a heterogeneous landscape including a branch system, sand and gravel banks, residual alluvial forests, swamps, lowland meadows, and agricultural land (BROZ 2007). Since the 19th century, parts of the Upper Danube Floodplain have been cleared for agricultural use (KONOLD 1993). Although the proportion of agricultural land decreased after the 1960s, it still maintains a high proportion along the Upper Danube (XU et al. 2017). Agricultural activities have been intensified since the implementation of the European Union's Common Agricultural Policy (HENLE et al. 2008). Riparian forests along the Upper Danube decreased from 1995 to 2010 because of river engineering projects (XU et al. 2017).

3.2.2 General approach

We analyzed the vegetation data from AuVeg, which is a vegetation database of German floodplains (HORCHLER et al. 2012). The vegetation records were collected in the context of the project "Variantenunabhängige Untersuchungen zum Ausbau der Donau zwischen Straubing und Vilshofen (Variant-independent investigations on the development of the Danube between Straubing and Vilshofen)" by the German Waterways and Shipping Administration (BfG 2013). The original selection of vegetation relevés aimed to cover the representative vegetation types present in the area and relevé size was determined following the Braun-Blanquet rules (BRAUN-BLANQUET 1964, BfG 2013). Among a large number of vegetation records along the Danube between Straubing and Vilshofen, we chose the relevés in the active and former floodplains sampled from 2010 to 2012 to represent the recent status. We selected the relevés of semi-terrestrial and terrestrial plant species with clear coordinate information. To avoid spatial autocorrelation, we set the minimum distance between relevés to 50 m (FAN & HSIEH 2010). Finally, 108 vegetation relevés (Fig. 3.1) were selected. This subset covers the most common vegetation types of the area.

To investigate the driving factors from the landscape to local level, we analyzed parameters of hydrology, land use, landscape structure, soil, and topography. In this study, the hydrological parameters were regarded as variables at the landscape level, because they reflect the river effects on the total floodplain. As for the parameters at the local level, we referred to the site characteristics (e.g., soil and topographic variables) of the relevé. Buffer zones of 500 m around the relevés were defined as a transitional level, where we focused on landscape composition and configuration. We set the buffer radius to 500 m to capture the direct effects of landscape structure in the vicinity of each relevé and at the same time to avoid overlap between buffer zones. We combined the vegetation and landscape to gain insight into the relationship between species composition and landscape patterns. The workflow is given in Fig. 3.2.

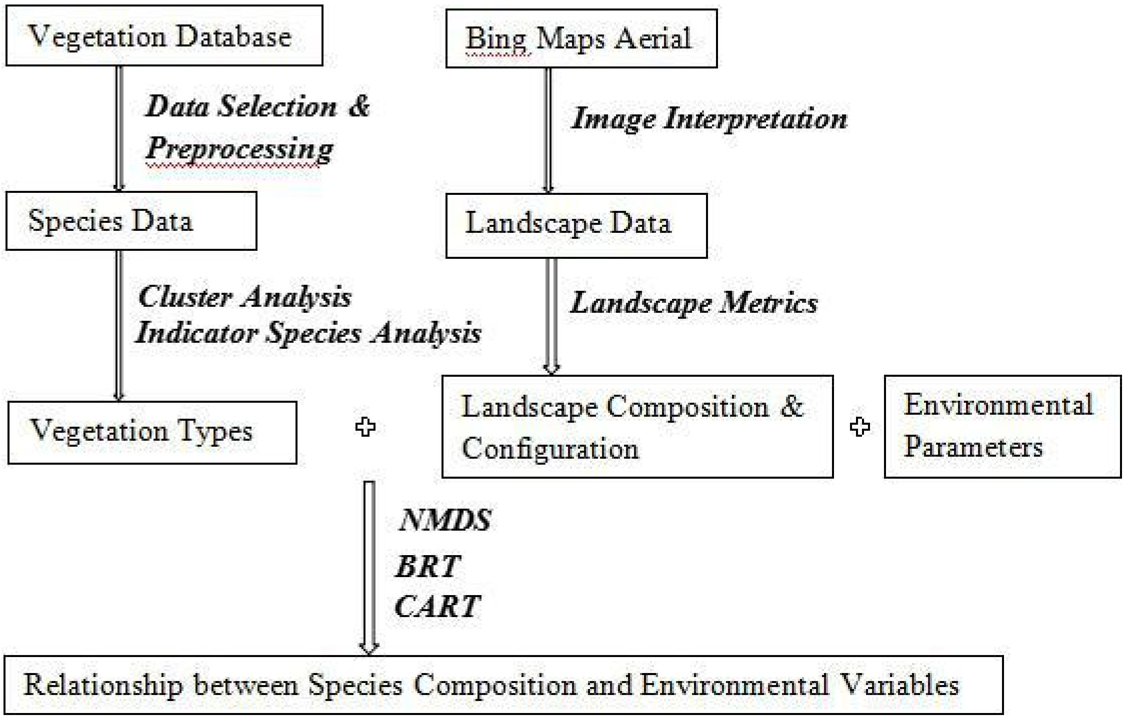


Fig. 3.2 The workflow of the study

Abb. 3.2 Der Arbeitsablauf der Studie

3.2.3 Analysis of vegetation data

We conducted hierarchical clustering of the relevés using the R package '*vegan*' (OKSANEN et al. 2013), which can display the similarity of samples across a wide range of scales and is not limited to the predetermined number of clusters. The percentage data of species cover were converted with the Hellinger and arcsine transformation, because this method is particularly suited for species cover data in multivariate studies (MCCUNE & GRACE 2002). The relevés were classified using the Bray-Curtis dissimilarity index (BRAY & CURTIS 1957), which accounts for the species cover data, best matches the ecological gradients, and is recommended for quantifying biotic homogenization (OLDEN & ROONEY 2006). We selected the complete-linkage clustering, in which the distance between clusters is defined as the distance between the two relevés that are farthest away from each other (LEGENDRE & LEGENDRE 1998).

Homogeneity within groups was tested with multi-response permutation procedures (MRPP, MIELKE & BERRY 2007). The p-values provide insight into the significance of each division.

The chance-corrected within-group agreement (A) describes homogeneity. If the emerging groups are significantly more homogeneous than expected by chance, then $1 > A > 0$ is true (McCune & Grace 2002).

An indicator species analysis (ISA) was performed to calculate indicator values for all species and their significances for the groups. The results determine the degree to which species are associated with the clusters. The analysis tests for statistical significance using the Monte Carlo test. The ISA was calculated using the *multipatt* function in the R package '*indicspecies*' (De C ceres & Legendre 2009). A threshold level of indicator value 25 with 95% significance (p-value $\leq$ 0.05) was set for identifying indicator species. The indicator species were used to characterize and name the vegetation types.

3.2.4 Analysis of environmental data

3.2.4.1 Analysis of the hydrological parameters

To describe the hydrological conditions at the landscape level, we selected the mean flooding duration (FD), depth to groundwater (GWFA_Flu), and flow velocity of a five-year flood (V-HQ5). These data were provided by BfG, the Rhein-Main-Donau AG (RMD), and the Federal Waterways Engineering and Research Institute (BAW; Table 3-A1). The reference period for the mean values (e.g., FD, GWFA_Flu) is from 1999 to 2008. The mean water level data (MW) were given as height a.s.l. and represented the long-term mean water level of observation sites. Height relative to MW (Height_MW) was defined as the difference between the absolute elevation a.s.l. of the relevé and the mean water level. Dist_Danube and Dist_WB referred to the distance from the relevé to the Danube and to the most adjacent water body, respectively.

3.2.4.2 Analysis of the landscape structural parameters

To analyze the landscape pattern around the relevés, we manually digitalized the land cover in the 500 m buffer zone around each relevé. This was performed in ArcGIS 10.2.1 (ESRI, Redlands, CA, USA) based on the Bing Maps Aerial in 2012 (30 cm resolution; © 2012 Microsoft Corporation).

According to the surface features, we classified the land cover into five primary groups: woody vegetation, agricultural land, water body, margin, and built-up land, which were divided into 21 subtypes by specific land use, structure, and vegetation cover (Table 3-A2).

We calculated land-cover configuration—shape, fragmentation, and isolation—as well as composition—proportion, richness, and diversity. To quantify these properties, we selected two indicators at the class level and five indicators at the landscape level (Table 3-A3). At the class level, the percentage of land cover (PLAND) and the number of patches (NP) describe landscape composition (McGarigal & Marks 1995). At the landscape level, the richness index (Rich_L) and the dominance index (Domi_L) quantify the richness and evenness of landscape composition (GOODWIN et al. 2017). Edge density (ED) and effective mesh size (MESH) were calculated to quantify fragmentation, because they are suitable for comparing the fragmentation of classes or landscapes with different total sizes (JAEGER 2000). To measure the fragmentation caused by infrastructure, we merged all other land uses and calculated the edge density of the landscape only caused by road, path, and vegetated paths. Landscape metrics of the land cover in the buffer zones were calculated using V-LATE (Vector-based Landscape Analysis Tool Extension for ArcGIS) 2.0 beta and FRAGSTATS v. 4.2.1 (MCGARIGAL & MARKS 1995, LANG & TIEDE 2003).

The concept of hemeroby quantifies the human impacts on vegetation, and it measures the distance between the current vegetation and a constructed state of self-regulating vegetation without human disturbances (WALZ & STEIN 2014). In this study, we applied this approach at the landscape level to investigate the degree of human impacts on the landscape. Hemeroby degrees were assigned to the land use types based on the previous assignment of hemeroby degrees to CORINE Land Cover classes (CLC) (WALZ & STEIN 2014, Table 3-A4).

3.2.4.3 Analysis of site-specific parameters

We used soil texture, content of sand, clay, humus, and carbonate in the upper soil layer, and thickness of loam layer as soil parameters at the local level (Table 3-A5). Based on the coordinates of the selected relevés, we extracted the soil data from the GIS-layers provided by the LDBV and the Rhein-Main-Donau AG (RMD).

The topographic parameters were slope, aspect, and distance to the road. Slope and aspect were extracted from the Digital Ground Model (DGM with 10 m resolution, provided by the Federal Agency for Cartography and Geodesy (BKG 2012). We transformed aspect to heat load index (HLI) with the following formula (MCCUNE & GRACE 2002):

$$\text{Heat load index} = [1 - \cos(\theta - 45)] / 2$$

where θ = aspect in degrees east of true north. This formula rescales aspect to a scale of zero to one, with zero being the coolest slope (northeast) and one being the warmest slope (southwest).

3.2.5 Combination of vegetation and environmental data

To interpret the species composition and test for the correlations between species composition and environmental variables, we conducted Non-Metric Multidimensional Scaling (NMDS) using the transformed species cover values of all relevés. The NMDS is an indirect ordination and gradient analysis method (TER BRAAK & PRENTICE 1988). It is flexible and uses the rank order (rather than the distance) to show the relationships among vegetation types. However, a distance metric must be specified to determine distance ranks at the beginning. We used the Bray-Curtis distance, 100 randomized runs with real data, a maximum of 500 iterations, and Procrustes rotation of three axes for the NMDS (implemented with the *metaMDS* function in the R package '*vegan*', OKSANEN et al. 2013). We fitted the environmental vectors and factors on the NMDS to assess their relations to species composition. The best linear fit to the ordination scores for each variable was determined, and the significance was tested with a permutation approach (implemented with the *envfit* function in the R package '*vegan*', OKSANEN et al. 2013). To avoid redundancy of predictors, we conducted a pairwise correlation test among the variables before fitting the data. The intercorrelated variables with a correlation coefficient higher than 0.7 were removed according to the rule of thumb (DORMANN et al. 2013). The correlation test reduced all the variables to 25 variables. The final list of environmental variables (Table 3.1) was a subset of the multiple variables estimated for each relevé (for the original list, see Table 3-A1, Table 3-A2, Table 3-A3).

Table 3.1 Environmental parameters included in the NMDS fitting.

Tabelle 3.1 Umweltparameter, die in der NMDS-Anpassung enthalten sind.

Group Variables	Variables	Units	Descriptions
Landscape level (the entire floodplain)			
Hydrological parameters	FD	d/a	Mean flooding duration (1999–2008)
	GWFA_Flu	cm	Depth to groundwater: mean water minus mean low water (1999–2008)
	V-HQ5	m/s	Flow velocity of a five-year flood
	Height_MW	m	Height relative to the mean water level (1999–2008)
	Dist_Danube	m	Distance to the river
	Dist_WB	m	Distance to the nearest water body
500 m buffer zone			

Landscape composition & configuration indices	Hemeroby_L	N/A	Landscape Hemeroby Index
	PLAND_agr	%	Percentage of agricultural land
	PLAND_bl	%	Percentage of built-up land
	Domi_LU	None	Dominant land use
	NP_gl	None	Number of grassland patches
	ED_i	m/ha	Edge density caused by the infrastructure
	MESH_L	ha	Landscape effective mesh size
	Rich_L	None	Landscape richness index
	Domi_L	None	Landscape dominance index
Local level			
Site land use	Site_LU	None	Site land use
Soil parameters	Soil_tx	None	Soil texture
	Soil_ty	None	Soil type
	Sand	%	Sand content in the upper soil
	Clay	%	Clay content in the upper soil
	Humus	%	Humus content in the upper soil
	Carbonate	%	Carbonate content in the upper soil
	ThLoam	cm	Thickness of loam layer in the profile
Topographic parameters	Slope	°	Slope
	HLI	None	Heat load index (derived from aspect)
	Dist_road	m	Distance to the nearest road/railway

The coefficient of determination (R^2) evaluates the goodness of fit for a set of data. For categorical variables, averages of ordination scores for factor levels were calculated.

Medians of the quantitative variables in groups of relevés were compared using the Kruskal-Wallis test.

To determine the variables related to species composition, we assessed the link between environmental variables and the main axes of species composition gained from the NMDS using Boosted Regression Trees (BRT) in the R package '*dismo*' (HIJMANS et al. 2017). The BRT combines machine learning with traditional regression approaches. Not being limited to simple linear relationships, the BRT is suitable to identify predictors for species distribution (ELITH et al. 2008). To avoid overfitting, we only used the significant variables from the fitting result of the NMDS as explanatory variables in the BRT. The model was conducted with cross-validation on data from 108 relevés using tree complexity of five and learning rate of 0.005. The bag fraction was set to the default value 0.5. We got the relative contributions (%) and rank of environmental variables for each NMDS axis from the BRT model.

We generated Classification and Regression Trees (CART) with the R package '*rpart*' (THERNEAU et al. 2015) to explore which environmental variables affect the occurrence of a species cluster. It is robust enough to handle categorical/numeric variables and represents the determinant factors through intuitive visualization (DE'ATH & FABRICIUS 2000). The group number G1–G10 was the target variable, 'gini' was selected as the split index, the complexity parameter was set to 0.001, and ten cross-validations were defined.

All the statistical analyses were performed in R version 3.1.0 (R CORE TEAM 2012).

3.3 Results

3.3.1 Vegetation types

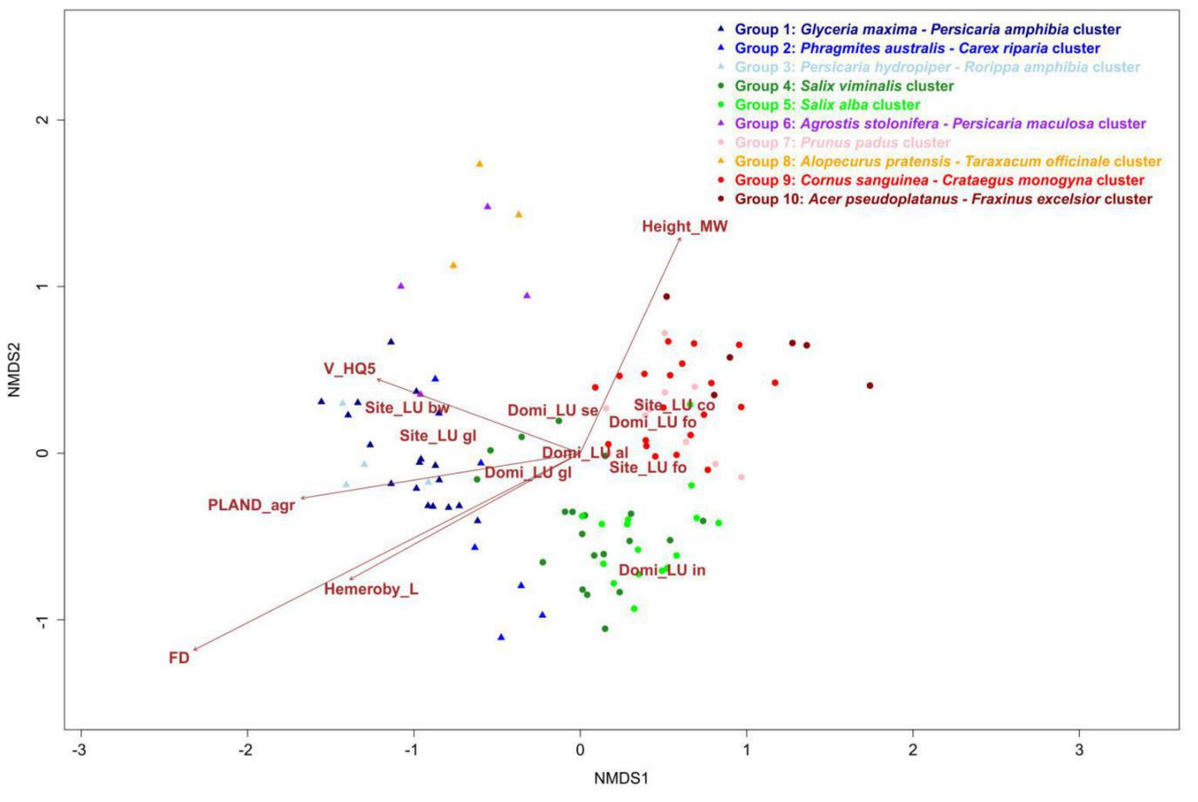
A total of 218 species (herbs, shrubs, and trees) were recorded in the 108 relevés. The species belong to 56 families and 146 genera. The families with the highest species richness were Poaceae (19 genera, 26 species), followed by Asteraceae (17 genera, 18 species), Brassicaceae (9 genera, 12 species), and Rosaceae (9 genera, 12 species).

The cluster analysis separated the relevés into ten groups, with 3 to 20 relevés per group (Table 3-A6). The MRPP test validated the number of clusters, with more homogeneity within groups than expected by chance (A = 0.2371, p-value = 0.001).

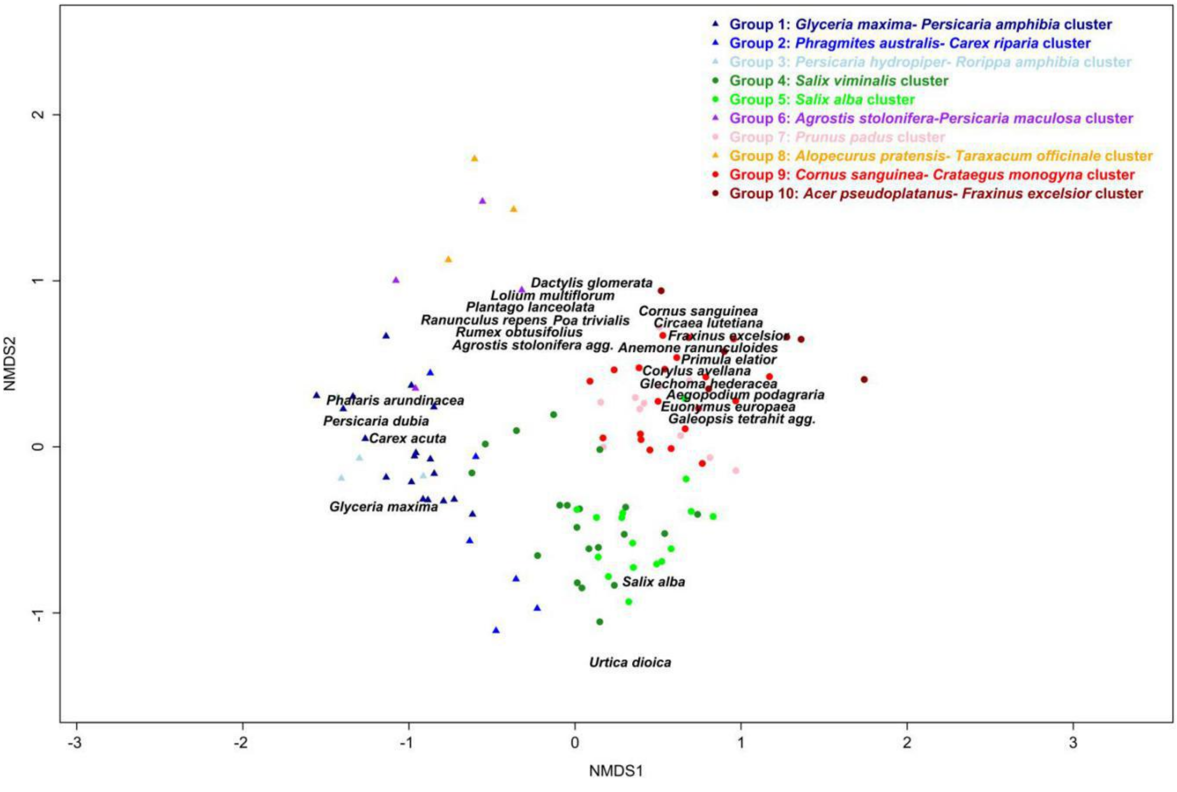
Groups 1 and 3 characterized the river bank vegetation. Group 2 was indicated mainly by reed species. There were two clusters indicated by the *Salix* species and two clusters dominated by the meadow species. Groups 7, 9, and 10 were characterized by shrub and tree species.

3.3.2 Relationship between environmental variables and species composition

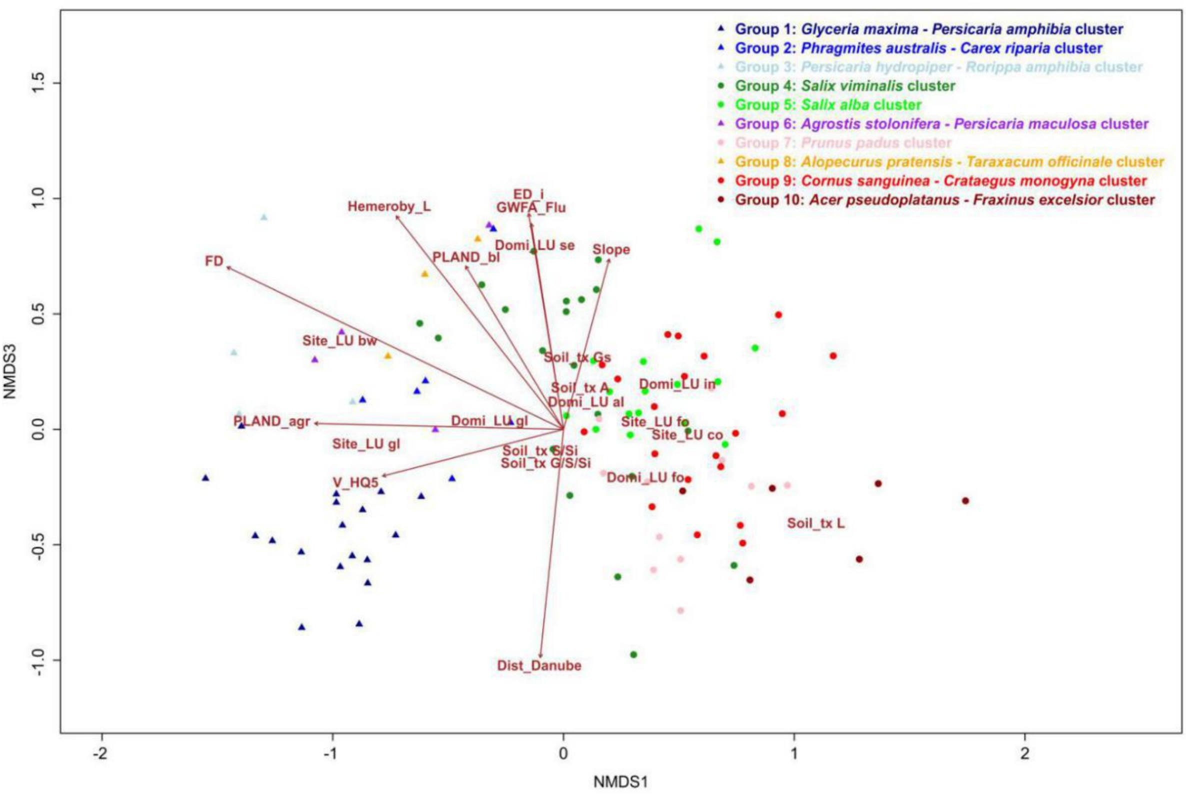
In the NMDS (Fig. 3.3), FD is the most important gradient along the 1st axis, followed by site openness and light. Species composition follows this gradient from an assemblage of hardwood forest to softwood forest then reed vegetation. PLAND_agr and V_HQ5 are highly negatively correlated to the 1st axis (Table 3.2). Height_MW is positively correlated to the 2nd axis (Table 3.2). The 3rd axis shows gradients at all levels: the hydrological gradients (e.g., Dist_Danube, GWFA_Flu), the landscape structural gradients (e.g., ED_i), and the topographic gradients (e.g., slope).



(a)


Group 1: Glyceria maxima- Persicaria amphibia cluster
Group 2: Phragmites australis- Carex riparia cluster
Group 3: Persicaria hydropiper- Rorippa amphibia cluster
Group 4: Salix viminalis cluster
Group 5: Salix alba cluster
Group 6: Agrostis stolonifera-Persicaria maculosa cluster
Group 7: Prunus padus cluster
Group 8: Alopecurus pratensis- Taraxacum officinale cluster
Group 9: Cornus sanguinea- Crataegus monogyna cluster
Group 10: Acer pseudoplatanus- Fraxinus excelsior cluster
Dactylis glomerata
Lolium multiflorum
Plantago lanceolata
Ranunculus repens Poa trivialis
Rumex obtusifolius
Agrostis stolonifera agg.
Cornus sanguinea
Circaea lutetiana
Fraxinus excelsior
Anemone ranunculoides
Primula elatior
Corylus avellana
Glechoma hederacea
Aegopodium podagraria
Euonymus europaea
Galeopsis tetrahit agg.
Phalaris arundinacea
Persicaria dubia
Carex acuta
Glyceria maxima
Salix alba
Urtica dioica
NMDS1
NMDS2

(b)


Group 1: Glyceria maxima - Persicaria amphibia cluster
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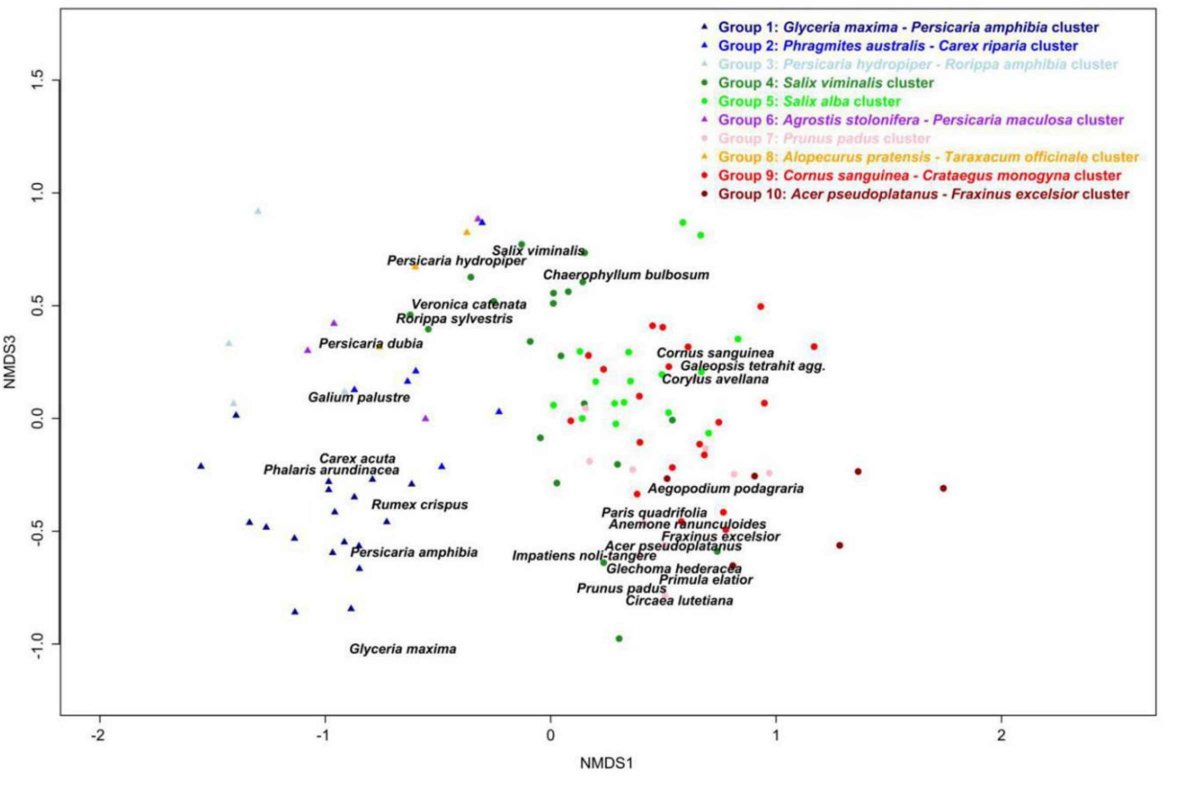
Group 7: Prunus padus cluster
Group 8: Alopecurus pratensis - Taraxacum officinale cluster
Group 9: Cornus sanguinea - Crataegus monogyna cluster
Group 10: Acer pseudoplatanus - Fraxinus excelsior cluster
ED_i
GWFA_Flu
Hemeroby_L
FD
Domi_LU se
Slope
PLAND_bl
Site_LU bw
Soil_tx Gs
Soil_tx A
Domi_LU al
Domi_LU in
PLAND_agr
Domi_LU gl
Site_LU gl
Site_LU fo
Site_LU co
Soil_tx G/Si
Soil_tx G/S/Si
V_HQ5
Domi_LU fo
Soil_tx L
Dist_Danube
NMDS1
NMDS3

(c)



(d)

Fig. 3.3 Non-Metric Multidimensional Scaling (NMDS) with fitted environmental variables and most frequent species. Graphs (a) and (b) display axes 1 and 2, while (c) and (d) display axes 1 and 3. The brown vectors in (a) and (c) show the direction of linear correlation of continuous variables with ordination scores (p-value ≤ 0.05). The brown dots in (a) and (c) stand for categorical variables (p-value ≤ 0.05). Graphs (b) and (d) show the most frequent species (p-value ≤ 0.001). The woody vegetation relevés are represented by circular markers, and the herbaceous vegetation relevés are triangular. The solution was reached with the minimum stress of 14.1 (54 iterations with random starting configurations in one to three dimensions). For abbreviations of environmental variables see Table 3.1. Supplements: Site_LU: fo = forest, bw = backwater, gl = grassland, co = copse; Domi_LU: al = arable land, fo = forest, gl = grassland, in = industrial land, se = settlements; Soil_tx: A = mixed soil texture with wide grain size spectrum (e.g., gravel, silt, clay), G/S/Si = gravel/sand/silt, L = loam, S/Si = sand/silt.

Abb. 3.3 Non-Metric Multidimensional Scaling (NMDS) mit angepassten Umweltvektoren und häufigsten Arten. (a) und (b) zeigen die Achsen 1 und 2 an, während (c) und (d) die Achsen 1 und 3 anzeigen. Die braunen Vektoren in (a) und (c) zeigen die Richtung der linearen Korrelation kontinuierlicher Umweltvariablen mit den Ordinationsachsen (p-Wert ≤ 0,05). Die braunen Punkte in (a) und (c) stehen für die kategorialen Umweltvariablen (p-Wert ≤ 0,05). (b) und (d) zeigen die häufigsten Arten (p-Wert ≤ 0,001). Die

Vegetationsaufnahmen aus Gehölzen sind kreisförmig und die Vegetationsaufnahmen mit Dominanz krautiger Arten sind dreieckig dargestellt. Die Lösung wurde mit einem minimalen Stress von 14,1 erreicht (54 Iterationen mit zufälliger Startkonfiguration in einer bis drei Dimensionen). Abkürzungen von Umweltvariablen siehe Tabelle 3.1; Ergänzungen: Site_LU: fo = Wald, bw = Altwasser, gl = Grünland, Co = Gehölz; Domi_LU: al = Ackerland, fo = Wald, gl = Grünland, in = Industriegebiet, se = Siedlung; Soil_tx: A = weites Korngrößenspektrum (z. B. Kies, Schluff, Ton), G/S/Si = Kies/Sand/Schluff, L = Lehm, S/Si = Sand/Schluff.

Table 3.2 Significant environmental variables fitted by the NMDS (Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05)

Tabelle 3.2 Korrelation signifikanter Umweltvariablen mit den NMDS-Achsen (Signif. Codes: 0 '***' 0.001 '**' 0.01 '*' 0.05)

Variables	**NMDS1**	**NMDS2**	**NMDS3**	**R^2**	**p**
Landscape level					
FD	-0.81878	-0.41655	0.39508	0.3789	0.001***
Dist_Danube	-0.09367	0.38114	-0.91976	0.1591	0.001***
GWFA_Flu	-0.14339	-0.37302	0.91668	0.1293	0.002**
Height_MW	0.42129	0.90653	-0.02666	0.1058	0.006**
V_HQ5	-0.91304	0.33272	-0.23590	0.0896	0.022*
500 m buffer zone					
Hemeroby_L	-0.58465	-0.32010	0.74547	0.1945	0.001***
PLAND_agr	-0.98695	-0.15933	0.02334	0.1500	0.001***
ED_i	-0.15151	-0.30538	0.94010	0.1321	0.003**
Domi_LU				0.1049	0.004**
PLAND_bl	-0.49347	-0.28168	0.82289	0.0946	0.014*
Local level					
Site_LU				0.3591	0.001***
Slope	0.24258	-0.35279	0.90371	0.0893	0.016*
Soil_tx				0.0753	0.024*

Thirteen variables are significantly related to the axes (p-value ≤ 0.05, Table 3.2). The most important parameters are hydrological, e.g., the mean flooding duration, followed by landscape hemeroby, edge density caused by infrastructure and land-use related parameters. Site-specific parameters (e.g., site land use) are also significant but explain only little variation.

The BRT results show the relative contributions of environmental variables (Table 3.3). The site land use explains the largest proportion of the variance of the 1st NMDS axis, while the height relative to the mean water level and flow velocity contribute to the highest variances of the 2nd and 3rd axes, respectively.

Table 3.3 The relative contributions (%) of environmental variables for the three NMDS ordination axes in the BRT model (abbreviations are explained in Table 3.1).

Tabelle 3.3 Die relativen Beiträge (%) der Umweltvariablen für die drei NMDS-Ordinationsachsen im BRT-Modell (Abkürzungen sind in Tabelle 3.1 erläutert).

	NMDS1 (explained deviance = 90.2 %)	**NMDS2 (explained deviance = 43 %)**	**NMDS3 (explained deviance = 75.9 %)**
Landscape level			
FD	15.3 %	12.8 %	8.3 %
GWFA_Flu	6.4 %	7.5 %	10.2 %
Height_MW	2.2 %	17.9 %	5.2 %
Dist_Danube	2.4 %	8.7 %	12.6 %
V_HQ5	2 %	15.9 %	12.7 %
500 m buffer zone			
PLAND_agr	3.4 %	5.1 %	8.8 %
Hemeroby_L	3.2 %	6.5 %	7.2 %
ED_i	1.9 %	5.7 %	8.6 %
PLAND_bl	1.6 %	4.4 %	7.9 %
Domi_LU	1.2 %	1.2 %	2.1 %
Local level			

Site_LU	55.7 %	6.6 %	2.1 %
Slope	2.8 %	1.7 %	4.1 %
Soil_tx	1.8 %	6.1 %	10.2 %

3.3.3 Habitat characteristics of vegetation types and the CART results

The habitat characteristics as defined by the results from the Kruskal-Wallis test (Table 3-A7) and the NMDS are described in detail in Table 3-A8.

Based on the CART results, there are 8 splits (9 terminal nodes) in the regression tree for the total dataset, and the R^2 value is 0.45 (Table 3.4, Fig. 3.4). The first split in the CART is determined by the land use. All other splits are determined by hydrological parameters (FD, V_HQ5) and landscape structural parameters indicating human influences either by land use activities (PLAND_agr), or landscape hemeroby. For example, areas with a high proportion of agricultural land have a larger number of relevés that are attributed to Group 1.

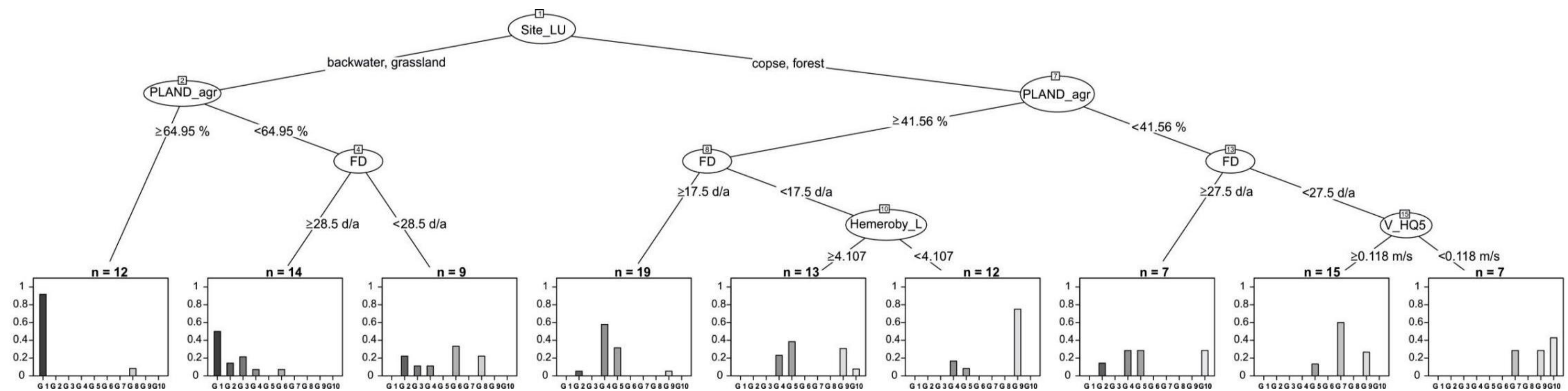


Fig. 3.4 The CART results of vegetation types and environmental factors. Abbreviations: G1: the *Glyceria maxima-Persicaria amphibia* cluster; G2: the *Phragmites australis-Carex riparia* cluster; G3: the *Persicaria hydropiper-Rorippa amphibia* cluster; G4: the *Salix viminalis* cluster; G5: the *Salix alba* cluster; G6: the *Agrostis stolonifera-Persicaria maculosa* cluster; G7: the *Prunus padus* cluster; G8: the *Alopecurus pratensis-Taraxacum officinale* cluster; G9: the *Cornus sanguinea-Crataegus monogyna* cluster; G10: the *Acer pseudoplatanus-Fraxinus excelsior* cluster. For abbreviations of the environmental variables see Table 3.1.

Abb. 3.4 Das CART Ergebnis von Artengruppen und Umweltfaktoren. Abkürzungen: G1: der *Glyceria maxima-Persicaria amphibia* Cluster; G2: der *Phragmites australis-Carex riparia* Cluster; G3: der *Persicaria hydropiper-Rorippa amphibia* Cluster; G4: der *Salix viminalis* Cluster; G5: der *Salix alba* Cluster; G6: der *Agrostis stolonifera-Persicaria maculosa* Cluster; G7: der *Prunus padus* Cluster; G8: der *Alopecurus pratensis-Taraxacum officinale* Cluster; G9: der *Cornus sanguinea-Crataegus monogyna* Cluster; G10: der *Acer pseudoplatanus-Fraxinus excelsior* Cluster. Für Abkürzungen der Umweltvariablen siehe Tabelle 3.1.

Table 3.4 The relative importance of the environmental variables for the distribution of vegetation types. (Note: Results were calculated with CART; the relative importance of environmental variables sums up to 100 and the digits after the decimal point were automatically omitted. For abbreviations, see Table 3.1.)

Tabelle 3.4 Die relative Bedeutung von Umweltvariablen für die Verteilung von Artengruppen. (Anmerkung: Die Ergebnisse wurden mit CART berechnet; die relative Bedeutung der Umgebungsvariablen beträgt in der Summe 100 und die Nachkommastellen wurden automatisch weggelassen. Abkürzungen siehe Tabelle 3.1.)

Environmental Variables	Relative Importance
FD	15
PLAND_agr	14
Site_LU	14
Hemeroby_L	8
Height_MW	8
V_HQ5	8
PLAND_bl	7
GWFA_Flu	7
Domi_LU	7
ED_i	4
Dist_Danube	3
Soil_tx	2
Slope	1

3.4 Discussion

3.4.1 What are the effects of hydrological parameters on species composition in the Danube Floodplain?

Among all the variables, the hydrological parameters were correlated most strongly with the species composition in the Danube Floodplain. This fits with other studies, in which the river regime and flow-mediated fluvial processes, especially the flooding duration and inundation levels, affect sediment dynamics, soil nutrients, and vegetation establishment

(OSTERKAMP & HUPP 2010, TSHEBOENG et al. 2014). Even in a floodplain with reduced hydrological dynamic, the hydrological conditions were still the most important environmental factors at the Danube River between Neuburg and Ingolstadt (LANG et al. 2011).

The mean flooding duration of the relevés ranged widely from 2 to 185 days per year. Not only the forests, but also the open habitats, followed the gradient of flooding duration due to different inundation tolerances. The wettest area with the longest flooding duration was occupied by the *Agrostis stolonifera-Persicaria maculosa* and *Persicaria hydropiper-Rorippa amphibia* clusters, which are tolerant of waterlogging and flooding in swamps and river banks. AHLMER (1989) describes both communities as moisture-preferring pioneers occurring frequently in the study area (especially the *Oenantho-Rorippetum* community with *Rorippa amphibia*). Wet meadows can develop when occasionally inundated. Following wet meadows along this gradient in decreasing moisture were the *Salix* clusters. Mature *Salix alba* individuals can withstand 190 days per year with the soil surface covered by water (DISTER 1983, LEUSCHNER & ELLENBERG 2017a). The shortest flooding duration occurred in the *Alopecurus pratensis-Taraxacum officinale*, *Prunus padus*, *Cornus sanguinea-Crataegus monogyna*, and *Acer pseudoplatanus-Fraxinus excelsior* clusters, which corresponds to the findings of AHLMER (1989) for this area along the Danube. The tree species in the hardwood forest have a moderate tolerance to the flooding regime and are not usually found on the permanently flooded soil. *Acer pseudoplatanus* and *Fraxinus excelsior* in the *Acer pseudoplatanus-Fraxinus excelsior* cluster have a relatively low flooding tolerance (e.g., *Fraxinus excelsior* along the Upper Rhine: about 40 days per year, *Acer pseudoplatanus*: less than 30 days per year; DISTER 1983, LEUSCHNER & ELLENBERG 2017a). This finding corresponds to the above mentioned floodplain between Neuburg and Ingolstadt, where *Fraxinus excelsior* and *Acer pseudoplatanus* were the most abundant tree species (LANG et al. 2011). *Cornus sanguinea* and *Crataegus monogyna* in the *Cornus sanguinea-Crataegus monogyna* cluster have low to medium flooding tolerances (GLENZ et al. 2006). The hydrological regimes of the waterways under strong human influences have been altered in different ways (HAMILTON 2002). In the free-flowing stretch of the Danube, there are dykes and embankments, but the species composition along this stretch still reflects a flooding gradient in the active floodplain.

In addition to the flooding duration, other variables such as depth to groundwater and height relative to the mean water level are proxies indicating the soil moisture within the root zone, which leads to the differences in species composition (BOOTH & LOHEIDE 2012). In our study, the river bank vegetation and reed clusters were closest to groundwater, while hardwood forests were the farthest. Species' adaptabilities to groundwater levels and fluctuations depend on their rooting depths and water source flexibilities. The groundwater levels under floodplain meadows and softwood forests were more fluctuating than other groups. The elevated sites with the shortest mean flooding duration and stable groundwater level were occupied by hardwood forests. HAGER & SCHUME (2001) found that less flood-tolerant species prefer the higher sites or those distant from the river. Some relevés of the river bank vegetation, reeds and softwood forests occurred below the mean water level. Their occurrences in the low-lying and frequently flooded sites result from the pioneer characteristics and adaptations to long flooding durations (HAGER & SCHUME 2001). Such low-lying areas (e.g., former river channels, relict creeks) are exposed to higher water levels, a higher flooding frequency, and longer flooding duration than the elevated patches (TOOGOOD et al. 2008).

The vegetation in the study area still reflects typical floodplain patterns and is driven by the hydrological regimes, even in the floodplain areas under strong human influences. However, land use, landscape structures, and soil conditions also influence the species distribution. In fact, the near-natural vegetation does not cover the whole floodplain, but only represents small remnants, also in atypical habitats.

3.4.2 What are the effects of landscape structural parameters on species composition in the Danube Floodplain?

Despite the strong hydrological differences that drive species distribution, landscape structural variables indicating human influences (e.g., land use activities, landscape hemeroby) are important to the species composition in the floodplain. In the study area, landscapes around softwood forests, reeds, and wet and mesic meadows were strongly fragmented by built-up land (e.g., infrastructure, settlements). While softwood stands are restricted to narrow belts along the river, riparian forests were nearly lost along the Upper Danube, covering only small fragments compared to the landscape in the 1960s (MARGRAF 2004, XU et al. 2017). This development was already visible in the 1980s (AHLMER 1989). Landscape hemeroby was high in the buffer zones around softwood remnants and floodplain meadows due to large proportions of built-up land (e.g., infrastructure, settlements) and agricultural land. The losses of natural floodplain forests were likewise found along other parts of the Danube, as well as other large rivers (e.g., the Morava) due to fragmentation caused by agricultural and built-up land (BROZ 2007, Š LEK et al. 2013). In our study, roads and other infrastructure were built close to the river, where the affected vegetation types mainly occurred. The proximity to waterways and settlements promotes the location of infrastructure along rivers to serve for transportation and recreation functions, especially in densely populated areas (FORMAN et al. 2003, BLANTON & MARCUS 2009). However, transportation infrastructure impairs natural habitat development and woody debris dynamics, and causes direct and indirect habitat loss for sensitive species (EIGENBROD et al. 2007). With different abiotic conditions, such as hydrological, topographic, soil conditions, and light exposure, the infrastructure creates a different surrounding environment (LAURANCE et al. 2009). It also modifies the vegetation structure and the successional processes in the vicinity (SILVA et al. 2017). Therefore, landscape structural perspective is important to analyze the floodplain vegetation, which was demonstrated by other studies (FERNANDES et al. 2011).

3.4.3 What are the effects of site-specific parameters on species composition in the Danube Floodplain?

Compared to other factors, site land use and soil characteristics at the local level were of minor but measurable importance to the species composition. Previous researches showed the filtering effects of local land use management on the composition of forest and grassland communities (WESCHE et al. 2012, JAKOVAC et al. 2016). The physical permanence and site stability are more influential than the substrate composition for the tree distribution in floodplains (HUENNEKE & SHARITZ 1986).

Like other large floodplains, the Danube Floodplain is preferred for agriculture because of its naturally high fertility. Landowners make land-use decisions according to different factors, e.g., topography, soil characteristics, and previous land use (ROBINSON 2004). For example, when they choose sites for agricultural use, the area with high water tables (within 0.3 m of the surface) cannot support arable cropping and is limited to grassland or non-agricultural land use (POSTHUMUS et al. 2010). The higher parts of floodplains are highly suitable for crop fields, while the lower parts are wet and more suitable for grazing (VERHOEVEN & SETTER 2009). The flood-tolerant crops (e.g., varieties of wheats, oats, barley, and maize) can only grow in the short-flooding area and if flooding takes place early in the growing season (VERHOEVEN & SETTER 2009). Loamy soils with the optimum combination of grain sizes are also preferred for agricultural uses (CROUSE 2017).

Soil texture affects the natural distribution of forest tree species and crop growth, because it governs many soil properties, e.g., the soil permeability, the water retaining capacity, and the ability to store nutrients available to plants (OSMAN 2013). For example, gravel layers impede the root growth, which further affects the ability to absorb water (SINGER et al. 2014). In the study area, soil textures varied among vegetation types. The *Acer pseudoplatanus-Fraxinus excelsior* cluster grew on the loamy soils. In hardwood forests, the fine-textured soil with high carbon content and thick, uniform sediments, indicates static flooding conditions (GRAF-ROSENFELLNER 2016). The gravelly/sandy/silty soil was typical for other vegetation types. The coarse soil with low carbon content under softwood remnants represented strong flooding dynamics. TURNER et al. (2004) found that the influences of soil variation on mature floodplain forests are obvious on the large spatial scale, while on the local scale, the soil variation is more important for the tree seedling establishment than for mature forests.

The main soil types in the study area were gleyic fluvisols and gleysols-calcaric fluvisols. Fluvisols are used for grazing and crop production (especially orchards). In upstream river parts, fluvisols are usually confined to narrow strips adjacent to the river (FAO, 1998). The occurrence of the *Phragmites australis-Carex riparia* cluster on the gleyic fluvisols was demonstrated in the study of IORDACHI & VAN ASSCHE (2014). They found that mixed reed beds with sedge species usually develop on gleyic soils. The prolonged water saturation associated with lack of aeration and poor rooting conditions makes gleysols unsuitable for most crops. Gleysols are covered with natural swamp forest or permanent grasses for low-intensive grazing (FAO, 1998). In this study, the soil types of the *Prunus padus* cluster were gleyic fluvisols and gleysols, which were typical for this cluster (DIERSCHKE et al. 1987). Fluvic cambisols occurred in the river bank vegetation, reeds, and softwood and hardwood forests. Most cambisols are used intensively because of their high agricultural performances, e.g., medium texture, high fertility, and water holding capacity (FAO, 1998). Cambisols with loamy, loamy-sandy substrate are suitable for mesic meadows. However, the soil types for the *Alopecurus pratensis-Taraxacum officinale* cluster were gleysols-calcaric fluvisols and gleyic fluvisols, which showed the shift of mesic meadows from the traditional habitat to the less-preferable areas in the floodplain. This shift is probably because cambisols are preferred for crop production so that the areas available for mesic meadows are limited to those with less-favorable soil conditions.

3.4.4 Where are the habitats for the vegetation types in the floodplain under strong human influences?

We found that the hydrological variables explained most of the variance in the species composition. In natural floodplains, the hydrological parameters, such as flooding duration and frequency, are the most important explanatory variables for the vegetation distribution (OSTERKAMP & HUPP 2010). Reeds, softwood and hardwood forests are the typical vegetation types along gradients of inundation and distances to the river (ELLENBERG 2009). In this study, the vegetation units and factors driving species distribution are comparable to those in natural floodplains; however, there are differences in the sizes and locations of habitats.

As for the species composition, the *Glyceria maxima-Persicaria amphibia* cluster is similar to the *Glycerietum maximae* Hueck 1931, which occurs mostly on the calcareous, muddy soils along the slow-flowing and nutrient-rich water bodies (OBERDORFER 1992a). In the study area, this high-hemeroby group occurred in the agricultural landscape close to backwater and gravel ponds, which was also reported by AHLMER (1989). These locations experience prolonged soil saturation due to the low elevation, high water level, and moderate water fluctuations (Table 3-A8). Formed by gravel mining and other excavation activities (NORMAN et al. 1998), the typical vegetation around the gravel ponds along the Danube is the vegetation of eutrophic water bodies, wet forests, creepers, hydrophilic therophytes, and perennial ruderals (OTTO 1992). These gravel ponds along river channels become the secondary habitats of the *Glyceria maxima-Persicaria amphibia* cluster, which was proved by OTTO (1992) and KOWALIK et al. (2014). They found frequent occurrences of *Glyceria maxima* and *Persicaria amphibia* close to the gravel ponds and ditches along the Danube.

The *Phragmites australis-Carex riparia* cluster and the *Persicaria hydropiper-Rorippa amphibia* cluster both occurred in the agriculture-dominant landscapes. The *Phragmites australis-Carex riparia* cluster is similar to the *Phragmitetum communis* Schmale 1939, which develops at the eutrophic/mesotrophic water bodies and is sensitive to mowing and strong floods. AHLMER (1989) states that the *Caricetum ripariae* Knapp et Stoffers 1962 is a secondary community replacing the *Phragmitetum communis* when sites are mown, but that is invaded by *Phragmites* when mowing ceases, so that transitional stages between both communities occur. This corresponds well to the results of our cluster analysis and might hint to a former agricultural use of the sites where this community was found. In our study, this group was located in the area with relatively slow water flow and close to the groundwater level. It preferred the gleyic fluvisols with a thick loam layer. Similar to previous studies (OBERDORFER 1992a), the water level in the sites of the *Phragmites australis-Carex riparia* cluster fluctuated less than that of the *Glyceria maxima-Persicaria amphibia* cluster. The groundwater fluctuated in the sites of the *Persicaria hydropiper-Rorippa amphibia* cluster, which is comparable to the semi-ruderal *Bidention tripartitae* Nordhagen 1940 or to an impoverished state of the *Oenantho-Rorippetum* Lohmeyer 1950 as described as a frequent form of this community in the study area by AHLMER (1989). As a pioneer community on the river bank, its typical habitat is equipped with sufficient nutrient, water, and light availability, as well as frequent disturbances to create bare ground necessary for germination (LEUSCHNER & ELLENBERG 2017b). AHLMER (1989) found that the *Oenantho-Rorippetum* had mainly developed for two or more years and was thus impoverished in species. This hints towards lacking water level fluctuations in the associated sites. In our study, this cluster developed at the bank of the main river channel, where the river regime provides the pioneer species with frequent disturbances. It also occurred along the ditches and construction sites in the landscape with strong fragmentation and high hemeroby, indicating strong human disturbances.

The *Salix viminalis* cluster occurred in the forest-dominant area with fluctuating groundwater levels. The species composition of this group was similar to that of the *Salicetum triandrae* Malcuit 1929, which was found between Regensburg and Straubing (ZAHLHEIMER 1979, AHLMER 1989). This community became relatively rare, because its habitat decreased to only narrow areas of steep embankments or disappeared entirely due to the river regulation (OBERDORFER 1992b). In the study area, *Salix alba* grew in small strips or gallery-like forest remnants along the river bank because of the infrastructure close to the river, as also reported by AHLMER (1989). Both softwood forests were located in an area with dense infrastructure (e.g., path, road) and settlements. Although the species composition was similar to the typical softwood forests, only galleries of willows were found along the Danube rather than the extensive forests. The strong human disturbances contributed to the habitat loss of the softwood forests.

The *Agrostis stolonifera-Persicaria maculosa* cluster grew in the grassland with long flooding duration and strong human disturbances. *Agrostis stolonifera* occurs in seasonally inundated grassland with high water level and in the margins of water bodies (LANSDOWN 2011). *Persicaria maculosa* typifies the muddy habitats, arable land, and built-up land. The composition of this cluster resembles that of the *Rorippo-Agrostietum stoloniferae* Moor 1958, which has been found in flooded grasslands along the Danube (M LLER 1961) and other rivers, such as the Rhine and the Neckar. These species tolerate frequent inundations, and they inhabit the depressions in floodplains (MARKOVIĆ 1973).

The *Alopecurus pratensis-Taraxacum officinale* cluster grew in the agriculture-dominant area with strong fragmentation. This cluster is similar to the *Arrhenatherion* Koch 1926, an endangered community of mesic meadows (*Alopecurus pratensis, Sanguisorba officinalis*, protected by the EU Habitats Directive LRT 6510). ZAHLHEIMER (1979) found this community in Regensburg along the Danube. Typical habitats of this community along the Danube almost disappeared and changed into arable land (ARGE DANUBIA 2012). In this study, the mesic meadow cluster grew in the area with short flooding duration and quite above the groundwater and mean water level.

The composition of the *Prunus padus* cluster is similar to that of the *Pruno-Fraxinetum* Oberdorfer 1953. The typical habitat is characterized by the high groundwater level (20–70 cm above mean groundwater) and stagnant or slowly seeping water (OBERDORFER 1993). In the fairly natural conditions of the Danube Floodplain near Vienna, *Prunus padus* prefers the shrub layer in the damper areas (ELLENBERG 2009). In this study, the group occurred in the sites with slow water flow and short flooding duration. It inhabited the forest area with low fragmentation. Compared to the typical habitats, these sites were higher above the groundwater and mean water level (about 1.2 m depth to the groundwater and 1.4 m above the mean water level). The lower water table and decreasing groundwater level in the *Pruno-Fraxinetum* could result from the dykes and river regulation (JANSEN et al. 2002).

The *Cornus sanguinea-Crataegus monogyna* cluster and the *Acer pseudoplatanus-Fraxinus excelsior* cluster occurred in the sites that were high above the groundwater level with short flooding duration and were under moderate to strong human impacts. *Acer pseudoplatanus* can be tolerant of less than 30 days of flooding (DISTER 1983, LEUSCHNER & ELLENBERG 2017a), and nowadays it occurs regularly in floodplains (personal observation). *Fraxinus excelsior* inhabits floodplain forests with clay-loam soils. In this study, this cluster was located on the sites with flat to gentle slopes, and grew on loamy gleysols or calcaric fluvisols. The composition of this cluster corresponds to the *Alno-Ulmion* Br.Bl. & Tx. 1943, but is not clearly related to either of its associations.

The species composition along the Upper Danube is similar to the typical floodplain vegetation we would expect under near-natural conditions. Under such circumstances, the floodplain vegetation is mainly disturbed by river dynamics (M LLER 1998). Despite the typical species composition, some vegetation types (e.g., softwood remnants) either lost their habitats or occurred in atypical habitats. The loss of the softwood forests can result from the landscape fragmentation caused by infrastructure. The short-lived species that typically occur at the river banks were confined to the banks of backwater and gravel ponds, due to the regulation of the main river channel. Agricultural production, flood protection, and timber exploitation are the main causes of anthropogenic changes to the floodplain vegetation.

3.5 Conclusion

We explored the hydrological, landscape structural, and site characteristics along the Upper Danube. In the floodplain under strong human influences, hydrological parameters, such as flooding duration, were still the essential driving forces structuring floodplain vegetation. Therefore, the natural spatial and temporal patterns of river flow rates, water levels, and run-off patterns must be maintained. Site land use determined by farmers had strong influences on the species composition. The loss of softwood habitats along the Danube River in the fragmented landscape was related to the dense infrastructure and intensified agriculture.

Factors at all levels need to be taken into consideration before starting a landscape or project planning process in floodplains. The exploration of the complex pattern of species composition and distribution in the Danube Floodplain is important for the preservation of riparian forests and floodplain grasslands, especially in the planning process of future conservation management and design of protected areas in the floodplain. Agriculture is the dominant land use in most floodplains, but to fulfill the diverse functions in the floodplains, a balance between different land uses should be established. Therefore, a multi-objective approach should be adopted in the land management to safeguard the diverse ecosystem functions in the floodplains.

Erweiterte deutsche Zusammenfassung

Einleitung:

Flussauen sind aufgrund ihrer raum-zeitlichen Dynamik und der daraus resultierenden Standortheterogenität von großer Bedeutung für die Biodiversität und damit verbundene ökologische Funktionen (WARD et al. 2002). Das hydrologische Regime und die menschlichen Aktivitäten beeinflussen die Vegetationsstruktur in Auenlebensräumen (SCHNEIDER 2010). Eine systematische Untersuchung der Landschaftsstruktur wurde jedoch selten in Studien zur Artenzusammensetzung einbezogen. Ziel dieser Studie ist es, die menschlichen Einflüsse auf die Vegetation der Auen aus einer landschaftsökologischen Perspektive zu analysieren.

Material und Methoden:

108 Vegetationsaufnahmen entlang der Donau von Straubing nach Vilshofen in Deutschland wurden mit Clusteranalyse und Indikatorartenanalyse (ISA) klassifiziert. Um die Umweltfaktoren (abiotische und landschaftliche Parameter) von der Landschaftsebene bis zur lokalen Ebene zu untersuchen, analysierten wir hydrologische Parameter, die Zusammensetzung und Struktur der Landschaft sowie standortspezifische Merkmale.

Unterschiede in den Artenzusammensetzungen zwischen den Vegetationsclustern wurden mittels Non-metric Multidimensional Scaling (NMDS) analysiert. Wir untersuchten die landschaftsökologischen Beziehungen zwischen der Artenzusammensetzung und den Umweltvariablen durch Anpassung der Variablen an die NMDS-Ordination, mittels Boosted Regression Trees (BRT) und Classification and Regression Trees (CART).

Ergebnisse:

Es wurden zehn Artengemeinschaften (z. B. Auenwiesen, Ufervegetation, Weichholz-Auenwälder und Hartholz-Auenwälder, Tab. 3.3) aus der Wald- und Offenlandvegetation identifiziert, welche das hydrologische Gefälle in der Aue widerspiegeln.

13 Variablen standen signifikant mit der Artenzusammensetzung in Beziehung (Tab. 3.4). Auf der Landschaftsebene waren meist hydrologische Parameter für die Artenzusammensetzung wichtig, z. B. die mittlere Überflutungsdauer, die mittlere Schwankung des Grundwasserstands, die Strömungsgeschwindigkeit bei HQ5, die Höhe über dem mittleren Wasserstand und die Entfernung zur Donau. Die strukturellen Parameter der Landschaft (z. B. die von der Infrastruktur verursachte Randliniendichte), die Landschaftszusammensetzung (z. B. die Prozentsätze der landwirtschaftlich genutzten Fläche und des bebauten Landes) und der Hemerobiegrad der Landschaft spielten ebenfalls eine wesentliche Rolle für die Artenzusammensetzung. Auf lokaler Ebene beeinflussten die Landnutzung und die Bodenart die Artenzusammensetzung. Basierend auf dem CART-Ergebnis (Tab. 3.6) waren die Flutdauer, der Prozentsatz der landwirtschaftlichen Fläche, die Landnutzung und der Hemerobiegrad der Landschaft die wichtigsten Determinanten für das Auftreten einer Artengemeinschaft.

Diskussion:

Auch in einer Aue, die vom Menschen stark beeinflusst und verändert wurde - wie in dem Untersuchungsgebiet - sind die großräumigen hydrologischen Faktoren für die Artenzusammensetzung noch immer am wichtigsten. Darüber hinaus spielen die Landschaftszerschneidung und die Landnutzung (z. B. Landwirtschaft) eine wichtige Rolle. Obwohl die Zusammensetzung der Artengemeinschaften auf der Ebene der Vegetationsaufnahme noch relativ naturnah ist, ist die Ausdehnung auf Reste geschrumpft (z. B. die Weichholz-Auenwaldreste). Die ursprünglichen Lebensräume sind durch infrastrukturell bedingte Landschaftszerschneidung beeinträchtigt oder verloren gegangen. Der Standort der flussnahen Infrastruktur wurde vor allem in dicht besiedelten Gebieten zur Versorgung von Freizeit- und Transportfunktionen genutzt (BLANTON & MARCUS 2009). Dies verändert jedoch die Vegetationsstruktur und beeinträchtigt die Entwicklung der natürlichen Lebensräume (SILVA et al. 2017). Außerdem treten bestimmte Artengemeinschaften in neu entstandenen Lebensräumen auf. So sind zum Beispiel die kurzlebigen Arten, die typischerweise an den Flussufern vorkommen, aufgrund der technischen Sicherung der Ufer der Donau auf die Ufer von Altarmen und Kiesweihern beschränkt. Das lokale Landnutzungsmanagement und die Bodeneigenschaften veränderten die Zusammensetzung und Lebensräume der Artengemeinschaften. Zum Beispiel wurden die Wiesen mittlerer Standorte von ihrem ursprünglichen Standort auf weniger für Ackerbau geeignete Gebiete in den Auen verschoben.

Fazit:

Die Umweltfaktoren auf allen Ebenen müssen bei der Landschafts- oder Projektplanung in Auen berücksichtigt werden. Obwohl die Landwirtschaft in den meisten Auen in

Mitteleuropa die vorherrschende Landnutzung ist, sollte ein Gleichgewicht zwischen verschiedenen Landnutzungen geschaffen werden, damit Auen ihre Ökosystemfunktionen erfüllen können.

Acknowledgments:

We would like to thank the German Federal waterway and shipping administration (BfG), the Bavarian State Office for Survey and Geoinformation (LDBV), the Bavarian Environment Agency (LfU), the Rhein-Main-Donau AG (RMD) and the Federal Waterways Engineering and Research Institute (BAW) for the data provision. We are thankful to all colleagues from the Division of Landscape Ecology and Landscape Planning for suggestions and discussion in the research process. We thank Samantha Serratore for proofreading our English. This study is funded by a Ph.D. scholarship to Fang Xu awarded by the China Scholarship Council (CSC) and we appreciate the financial support.

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Summary

Due to high spatio-temporal heterogeneity, floodplains are of high importance for ecological functions (e.g., as a buffer of flood events, erosion control, wood producers and pollutant filters but also as a provider of important habitats). During the past centuries, large areas of European floodplains have gone lost and many riparian habitats (e.g., riparian forests, floodplain grassland) have been threatened by human activities. The land-cover change along the Upper Danube from 1963 to 2010 as well as the distribution pattern of floodplain vegetation at different scales were analysed to quantify the human influences on the floodplain landscapes and vegetation.

Landscapes in the Upper Danube Floodplain experienced an increasing fragmentation from 1963 to 2010, which resulted from agricultural intensification and infrastructure development (Chapter 2). Despite the decline of agricultural land in the floodplain in recent decades, it still accounted for a large proportion in the active floodplain due to agricultural intensification. The loss of riparian forests was a consequence of infrastructure development and forest clearance for flood protection. The land-cover transformation was mainly determined according to the hydrological, topographical and soil characteristics.

The distribution and composition of plant communities in floodplains is a consequence of both natural (e.g., hydrological and geomorphological) and human factors (Chapter 3). The analysis indicated that in the Danube Floodplain under strong human influences, hydrological parameters were still the primary driving forces causing the distribution pattern of floodplain vegetation. Landscape structure as well as fragmentation played an essential role in the distribution pattern of floodplain vegetation. The rare occurrence of softwood remnants along the Danube in the fragmented landscape resulted from the dense infrastructure and intensified agriculture. Backwater and gravel ponds proved to be secondary habitats for the short-lived species (e.g., *Glyceria maxima, Persicaria amphibia*), which originally occurred at river banks. Besides the hydrological factors and landscape patterns, site characteristics such as site land use, soil texture and soil types were of minor but measurable importance to the species composition.

Land-cover change led to the habitat loss of riparian forests and resulted in the shift of spatial distribution of some species groups. Due to the lack of historical vegetation data, the temporal comparison of species composition could not be conducted. However, based on previous researches it can be assumed that the increasing fragmentation might alter the species composition of floodplain vegetation, and the further fragmentation might become a problem in the future.

Overall, the results suggest that in the floodplain under strong human interventions, analysing the landscape pattern is a useful tool for explaining the plant species composition and the distribution of floodplain vegetation. A quantitative analysis of the temporal and spatial pattern of land cover, the distribution of floodplain communities such as forests and meadows from the landscape scale to the local scale provides a framework for analyzing landscape patterns in floodplains from a comprehensive view, and demonstrates the negative impacts of infrastructure development on the riparian habitats and floodplain vegetation.

Zusammenfassung

Aufgrund der hohen räumlichen und zeitlichen Dynamik sind die Auen von hoher Bedeutung für ihre ökologischen Funktionen (z. B. als Puffer von Überflutungsereignissen/Hochwässern, Erosionsschutz, Holzproduzent und Schadstofffilter aber auch als Bereitsteller von wichtigen Lebensräumen). In den vergangenen Jahrhunderten sind große Teile der europäischen Auen verloren gegangen und viele Auenlebensräume wurden durch menschliche Aktivitäten bedroht. Um die menschlichen Einflüsse auf die Auenlandschaften und die Auenvegetation zu quantifizieren, wurde der Landbedeckungswandel entlang der Oberen Donau von 1963 bis 2010 sowie das Verbreitungsmuster der Auenvegetation auf verschiedenen Skalen analysiert.

Die Landschaften in der Oberen Donauaue erlebten von 1963 bis 2010 eine zunehmende Fragmentierung, die aus der Intensivierung der Landwirtschaft und der Infrastrukturentwicklung resultierte (Kapitel 2). Trotz des Rückgangs der landwirtschaftlichen Fläche in den Auen in den letzten Jahrzehnten, blieb der Anteil landwirtschaftlicher Nutzfläche in den aktiven Auen, bedingt durch die landwirtschaftliche Intensivierung, relativ hoch. Der Verlust von Auwäldern war eine Folge der infrastrukturellen Entwicklung und der Waldräumung für den Hochwasserschutz. Die Landnutzungsänderungen wurden hauptsächlich durch die hydrologische und topografische Eigenschaften, sowie die Bodeneigenschaften bestimmt.

Die Verbreitung und die Zusammensetzung der Pflanzengesellschaften in den Auen ist eine Konsequenz der natürlichen (z. B. hydrologischen und geomorphologischen) und menschlichen Einflussfaktoren (Kapitel 3). Die Analyse zeigte, dass in der stark von menschlichem Handeln beeinflussten Donau-Aue die hydrologischen Parameter immer noch die Haupttriebkräfte der Verbreitungsmuster der Auenvegetation waren. Landschaftsstruktur ebenso wie Fragmentierung spielten eine wesentliche Rolle im Verteilungsmuster der Auenvegetation. Die seltenen Weichholz-Auen Fragmente in der zerschnittenen Landschaft der Donau-Aue resultieren aus der dichten Infrastruktur und der intensivierten Landwirtschaft.. Die Altwasser und die Kiesweiher erwiesen sich als sekundäre Lebensräume für die kurzlebigen Pflanzengemeinschaften, die ursprünglich an den Flussufern auftraten. Neben den hydrologischen Faktoren und den Landschaftsmustern waren lokale Merkmale wie Landnutzung, Bodenarten und Bodentypen für die Artenzusammensetzung von geringer, aber messbarer Bedeutung.

Der Landbedeckungswechsel/Landnutzungsänderungen führten zum Verlust der Auwälder und war gleichzeitig die Ursache für eine Verschiebung der räumlichen Verbreitung einiger Artengruppen. Aufgrund fehlender historischer Vegetationsdaten konnte der zeitliche Vergleich der Artenzusammensetzung nicht durchgeführt werden. Aufgrund der bisherigen Forschungen lässt sich annehmen, dass die zunehmende Fragmentierung die Artenzusammensetzung der Auenvegetation verändern könnte und die voranschreitende Fragmentierung in Zukunft ein Problem werden könnte.

Insgesamt deuten die Ergebnisse darauf hin, dass in den stark anthropogen geprägten Auen die Quantifizierung des Landschaftsmustersdie Artenzusammensetzung und die Verteilung der Auenvegetation erklären kann. Eine quantitative Analyse des zeitlichen und räumlichen Landnutzungsmusters, welches Verteilung von Auengesellschaften wie Wälder und Wiesen von der regionalen Skala zur lokalen Skala umfasst, bietet einen breiten Rahmen um zeigt die negativen Auswirkungen der Infrastrukturentwicklung auf die Auenlebensräume und Auenvegetation.

Acknowledgements

I would like to express my gratefulness to my supervisor Prof. Dr. Dr. habil. Dr. h.c. (TSU) Annette Otte. She accepted me as a doctoral student in the Division of Landscape Ecology and Landscape Planning, and she gave me the chance to join the working group of floodplain ecology. She supported me with excellent instructions and encouraged me with full patience. There is a Chinese saying: he who teaches me for one day is my father for life. Therefore, I appreciate all her help and guidance which would be a life-long treasure for me.

Many thanks go to Prof. Dr. Jan Siemens for his willingness to agree to be my second supervisor and evaluating my thesis.

I would like to thank the China Scholarship Council (CSC) for providing me with a PhD scholarship and Prof. Dr. Dr. habil. Dr. h.c. (TSU) Annette Otte for funding my dissertation after the termination of the Chinese scholarship.

Special thanks go to Dr. Sarah Harvolk-Schöning, Dr. Kristin Ludewig and PD. Dr. Tobias W. Donath for their great contributions to my study. I want to express my sincerely appreciation to all the colleagues in the Division of Landscape Ecology and Landscape Planning for their kindness and the motivated working atmosphere.

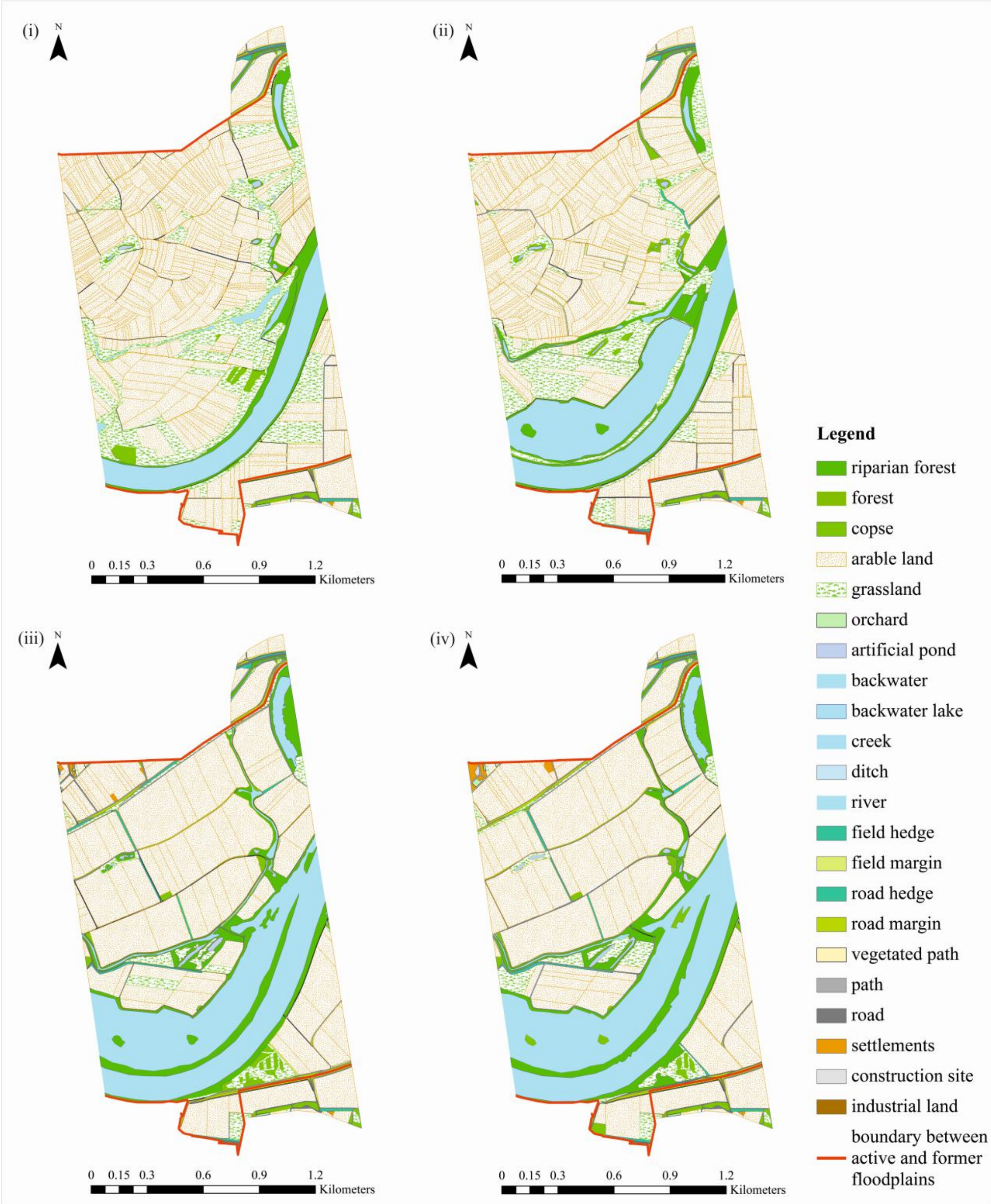
A special gratitude goes out to Dr. Peter J. Horchler from the German Federal waterway and shipping administration (BfG) for providing me with the vegetation data and giving me many helpful suggestions in the research process.

I am very grateful to my family members and friends. If not for their support and encouragement, I could not have finished this thesis. May my dearest grandfather rest in peace.

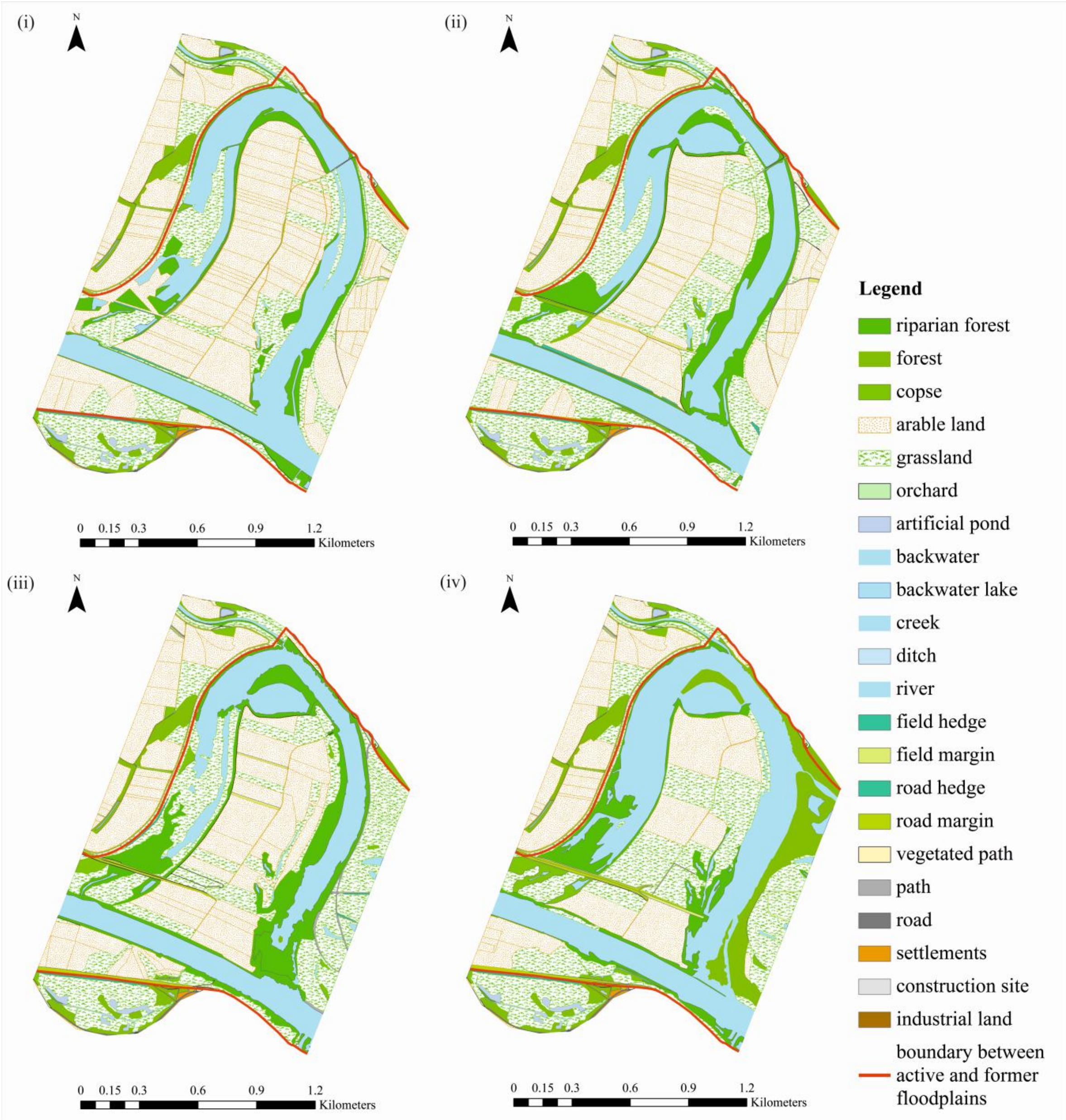
Appendix

Table 2-A1. Selected types of land cover change of arable land (A), grassland (G) and riparian forest (R).

Abbreviation (Alphabetic Order)	**Description**
AA	Stable arable land
A-G	Arable land to grassland
A-R	Arable land to riparian forest
A-F	Arable land to other forests
A-E	Arable land to other land cover
GG	Stable grassland
G-A	Grassland to arable land
G-R	Grassland to riparian forest
G-F	Grassland to other forests
G-E	Grassland to other land cover
RR	Stable riparian forest
R-A	Riparian forest to arable land
R-G	Riparian forest to grassland
R-F	Riparian forest to other forests
R-E	Riparian forest to other land cover


(i)
(ii)
(iii)
(iv)
N
0 0.15 0.3 0.6 0.9 1.2 Kilometers
Legend
riparian forest
forest
copse
arable land
grassland
orchard
artificial pond
backwater
backwater lake
creek
ditch
river
field hedge
field margin
road hedge
road margin
vegetated path
path
road
settlements
construction site
industrial land
boundary between active and former floodplains

(**a**)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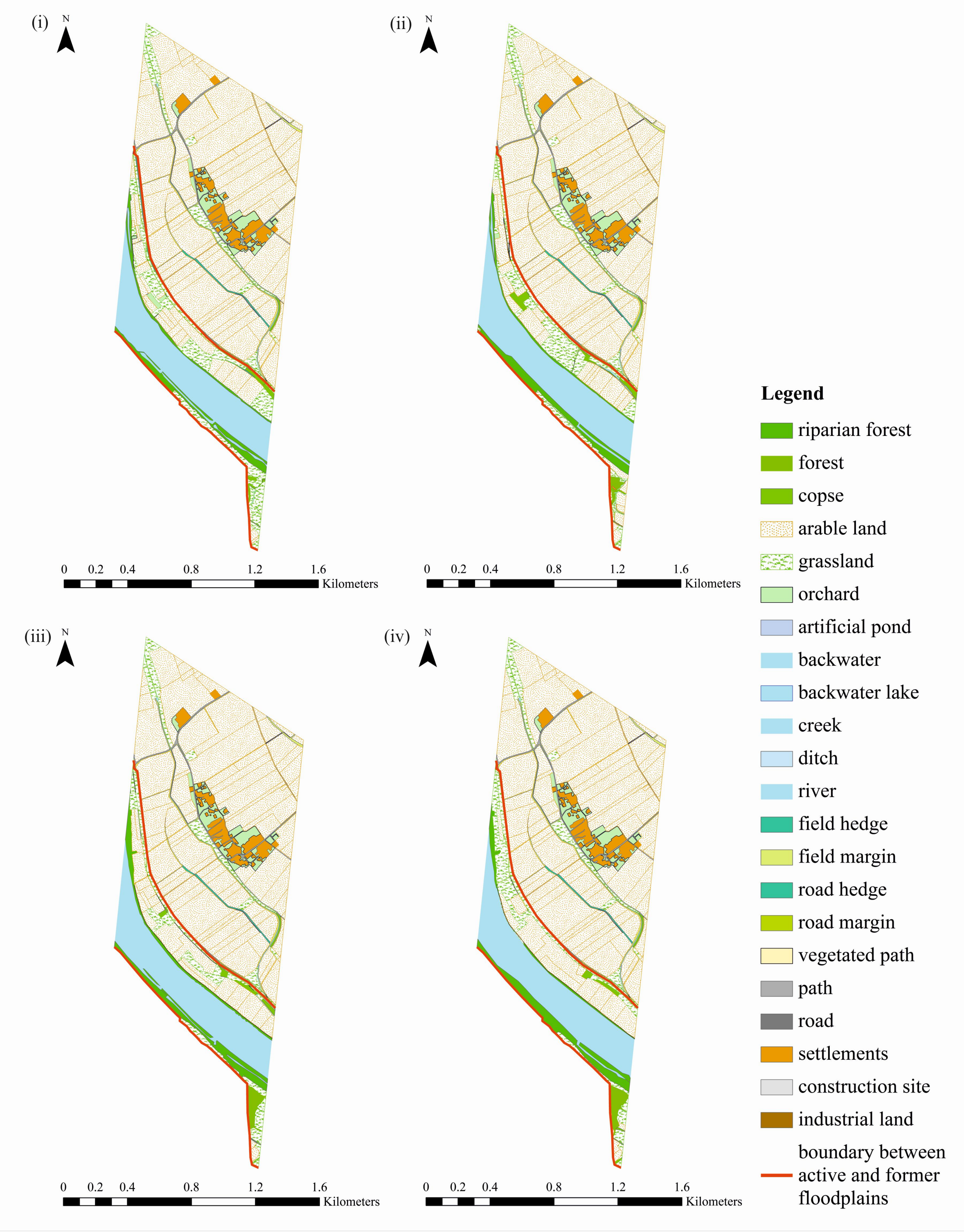
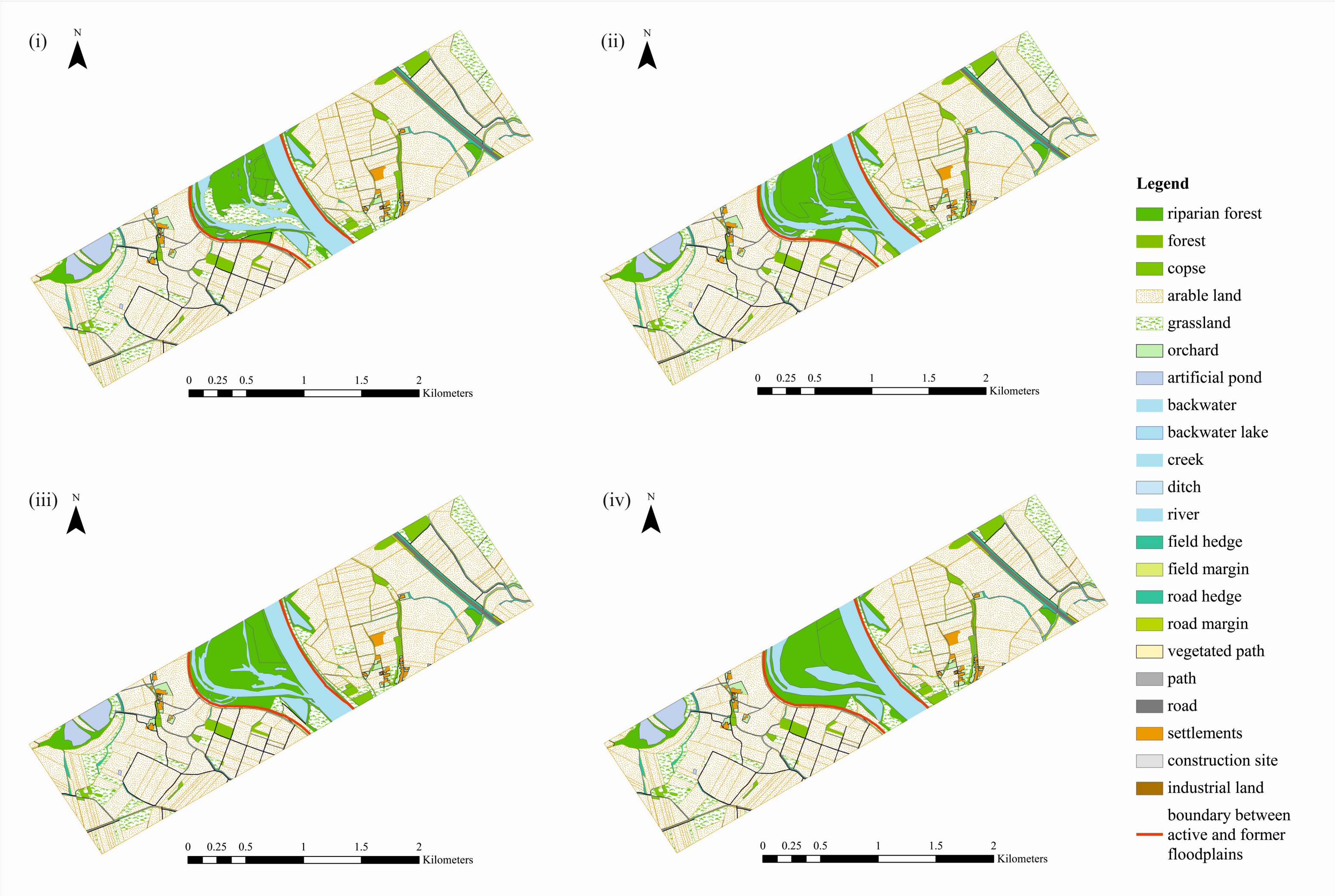
N
0 0.15 0.3 0.6 0.9 1.2
Kilometers
(iv)
N
0 0.15 0.3 0.6 0.9 1.2
Kilometers
Legend
riparian forest
forest
copse
arable land
grassland
orchard
artificial pond
backwater
backwater lake
creek
ditch
river
field hedge
field margin
road hedge
road margin
vegetated path
path
road
settlements
construction site
industrial land
boundary between active and former floodplains

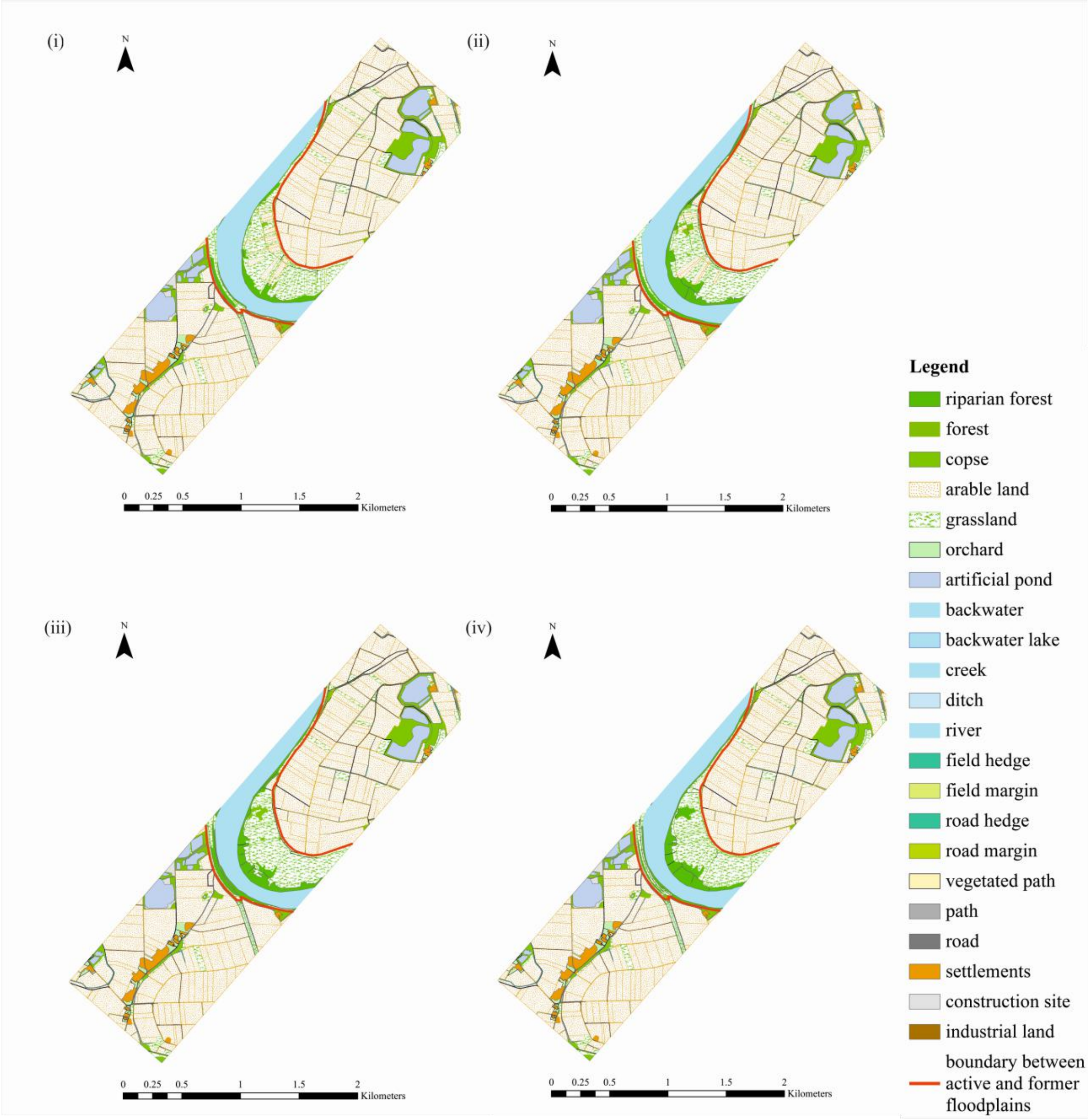
(**b**)


(i)
N
0 0.2 0.4 0.8 1.2 1.6 Kilometers
(ii)
N
0 0.2 0.4 0.8 1.2 1.6 Kilometers
(iii)
N
0 0.2 0.4 0.8 1.2 1.6 Kilometers
(iv)
N
0 0.2 0.4 0.8 1.2 1.6 Kilometers
Legend
riparian forest
forest
copse
arable land
grassland
orchard
artificial pond
backwater
backwater lake
creek
ditch
river
field hedge
field margin
road hedge
road margin
vegetated path
path
road
settlements
construction site
industrial land
boundary between active and former floodplains

(c)


(i)
N
0 0.25 0.5 1 1.5 2
Kilometers
(ii)
N
0 0.25 0.5 1 1.5 2
Kilometers
(iii)
N
0 0.25 0.5 1 1.5 2
Kilometers
(iv)
N
0 0.25 0.5 1 1.5 2
Kilometers
Legend
riparian forest
forest
copse
arable land
grassland
orchard
artificial pond
backwater
backwater lake
creek
ditch
river
field hedge
field margin
road hedge
road margin
vegetated path
path
road
settlements
construction site
industrial land
boundary between active and former floodplains

(d)



(**e**)

Figure 2-A1. An overview of land cover structure in the active and former floodplains of all study sites: (**a**) Barbing; (**b**) Gmünd; (**c**) Irlbach; (**d**) Niederalteich and (**e**) Langkünzig during all the periods (i. 1963; ii. 1978; iii. 1995; iv. 2010).

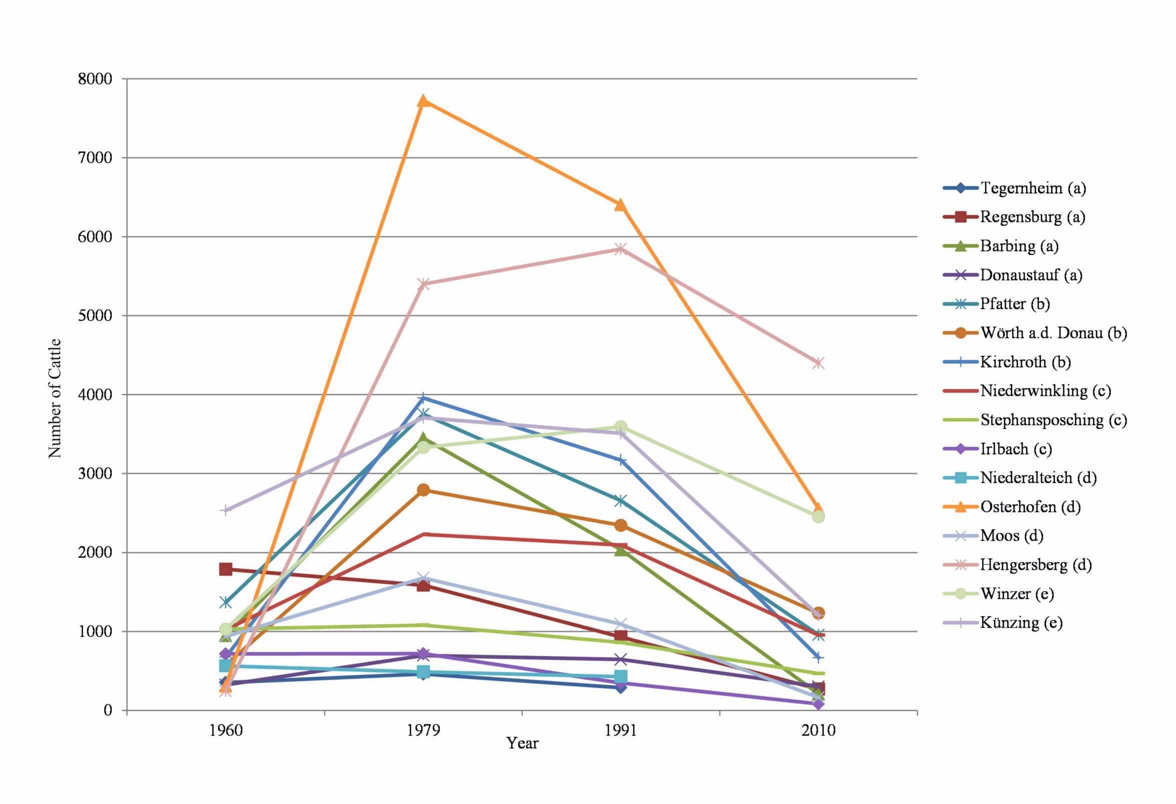
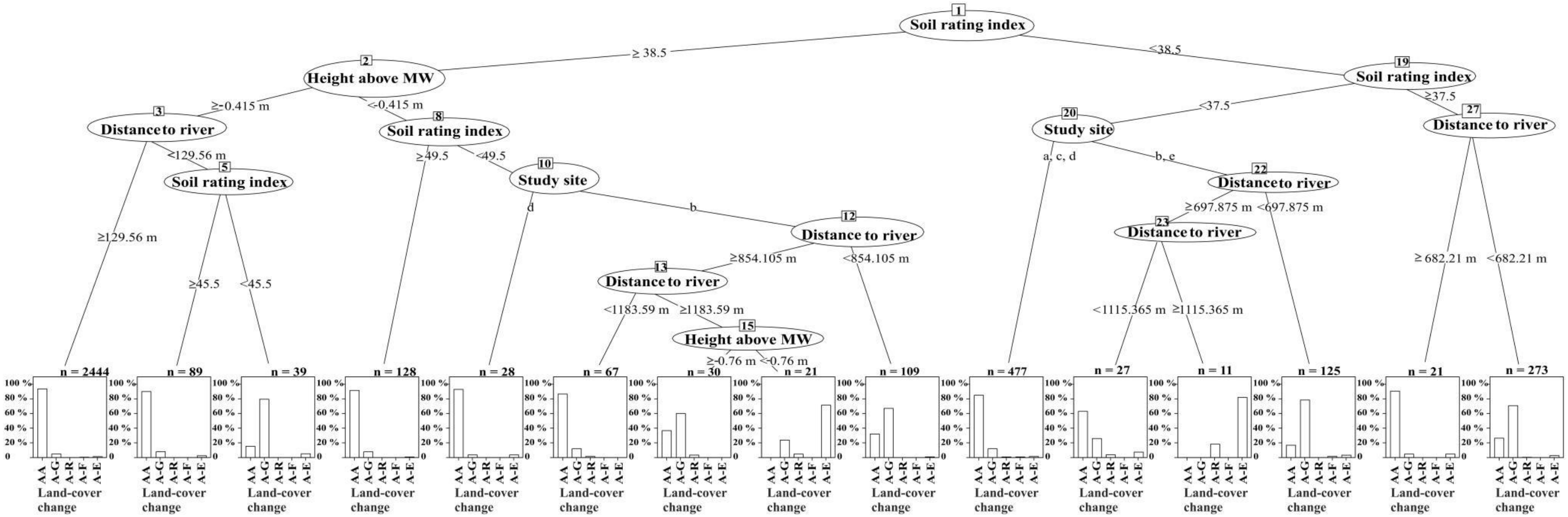
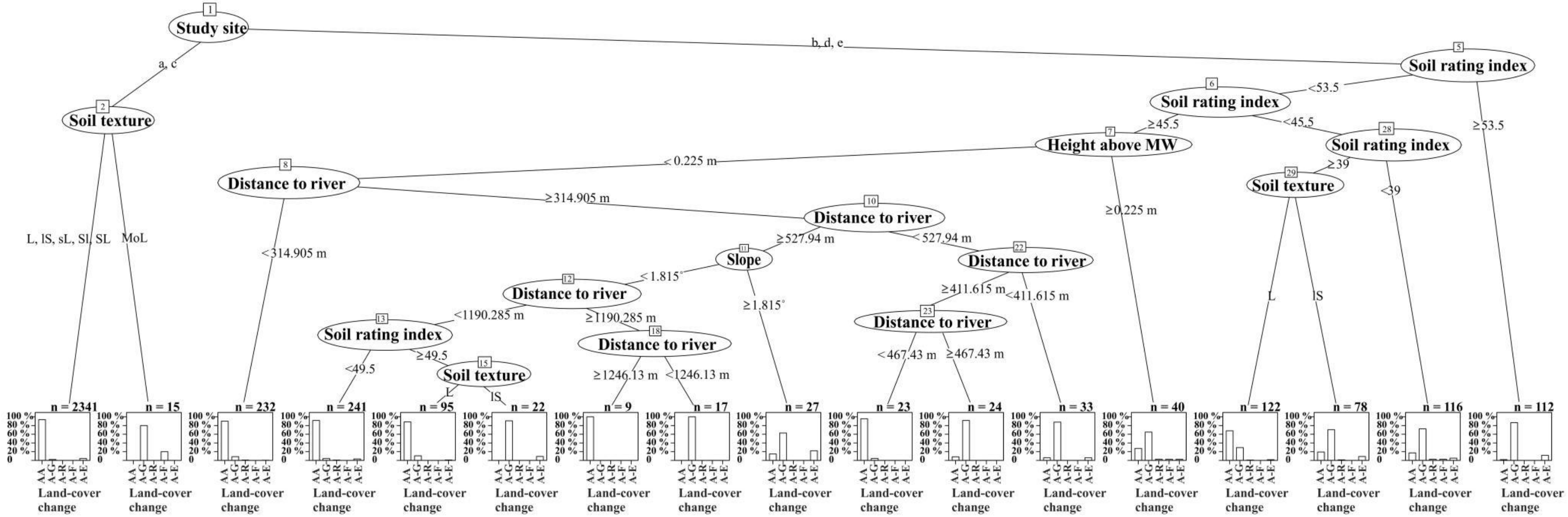


Figure 2-A2. The cattle number of 1960, 1979, 1991 and 2010 in all the municipalities of the study area [107]. The small letters refer to the study sites, see Fig. 2.1.

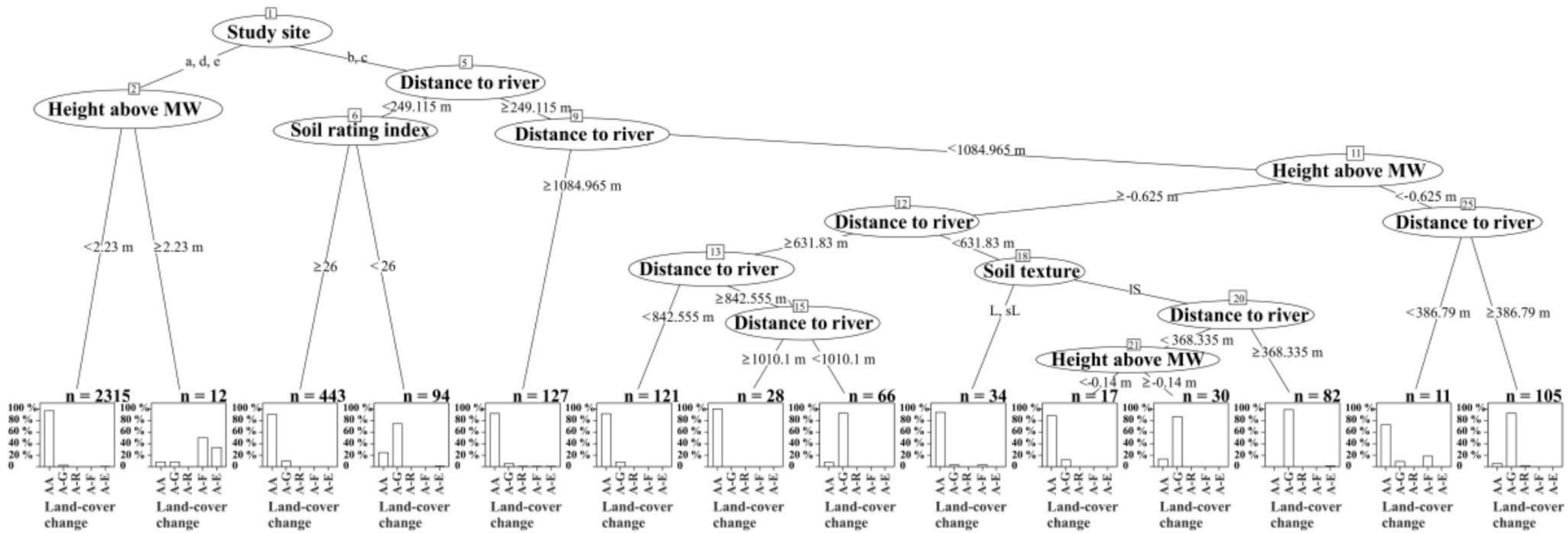


Soil rating index
≥ 38.5
<38.5
Height above MW
Soil rating index
≥-0.415 m
<-0.415 m
<37.5
≥37.5
Distance to river
Soil rating index
Study site
Distance to river
≥129.56 m
<129.56 m
≥49.5
<49.5
a, c, d
b, e
Soil rating index
Study site
Distance to river
d
b
Distance to river
≥697.875 m
<697.875 m
Distance to river
≥854.105 m
<854.105 m
Distance to river
≥45.5
<45.5
≥ 682.21 m
<682.21 m
<1183.59 m
≥1183.59 m
<1115.365 m
≥1115.365 m
Height above MW
≥-0.76 m
<-0.76 m
n = 2444
n = 89
n = 39
n = 128
n = 28
n = 67
n = 30
n = 21
n = 109
n = 477
n = 27
n = 11
n = 125
n = 21
n = 273
Land-cover change

(a)

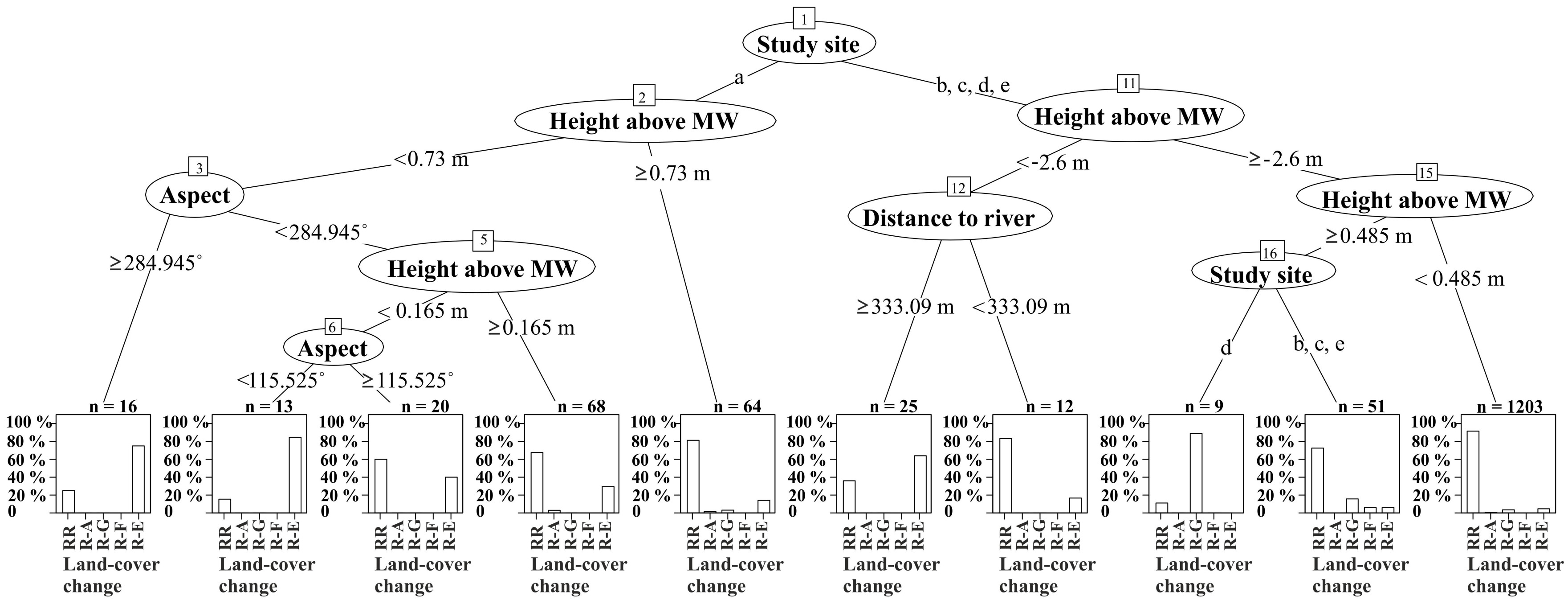

Study site
a, c
b, d, e
Soil texture
Soil rating index
<53.5
≥53.5
Soil rating index
≥45.5
<45.5
Height above MW
Soil rating index
<0.225 m
≥0.225 m
≥39
<39
Distance to river
Soil texture
L, lS, sL, Sl, SL
MoL
<314.905 m
≥314.905 m
Distance to river
≥527.94 m
<527.94 m
Slope
Distance to river
<1.815°
≥1.815°
Distance to river
≥411.615 m
<411.615 m
<1190.285 m
≥1190.285 m
Distance to river
Soil rating index
Distance to river
<467.43 m
≥467.43 m
<49.5
≥49.5
Soil texture
L
lS
≥1246.13 m
<1246.13 m
n = 2341
n = 15
n = 232
n = 241
n = 95
n = 22
n = 9
n = 17
n = 27
n = 23
n = 24
n = 33
n = 40
n = 122
n = 78
n = 116
n = 112
Land-cover change

(**b**)

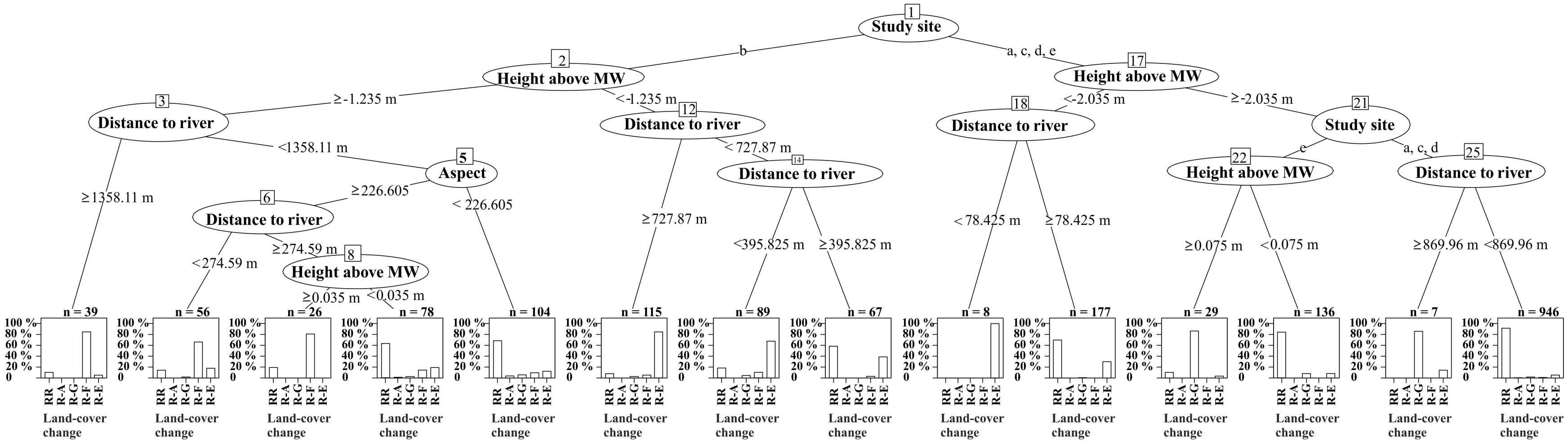


(**c**)

Figure 2-A3. The CART result of arable land change and environmental factors ((**a**) 1963–1978; (**b**) 1978–1995; (**c**) 1995–2010). Abbreviations: AA: stable arable land; A-G: arable land to grassland; A-R: arable land to riparian forest; A-F: arable land to other forests; A-E: arable land to other land cover; S: sand; Sl & lS: loamy sand; SL: very loamy sand; sL: sandy loam; L: loam; MoL: moor/loam, soil consisting of peat and loam; the small letters refer to the study sites, see Fig. 2.1.

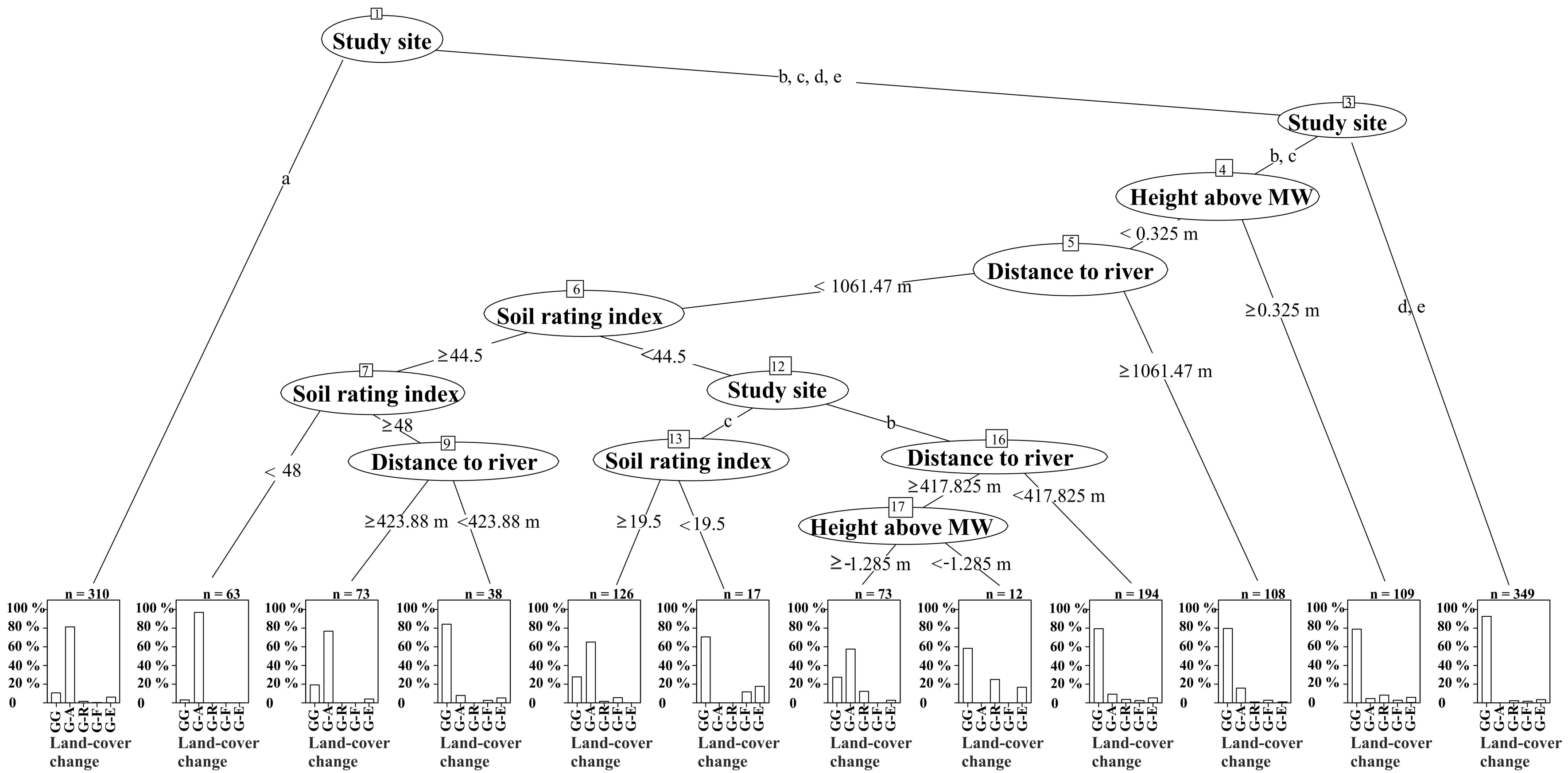

1
Study site
a
b, c, d, e
2
Height above MW
11
Height above MW
<0.73 m
≥0.73 m
<-2.6 m
≥-2.6 m
3
Aspect
12
Distance to river
15
Height above MW
≥284.945°
<284.945°
5
Height above MW
≥333.09 m
<333.09 m
≥0.485 m
< 0.485 m
16
Study site
< 0.165 m
≥0.165 m
6
Aspect
d
b, c, e
<115.525°
≥115.525°
n = 16
n = 13
n = 20
n = 68
n = 64
n = 25
n = 12
n = 9
n = 51
n = 1203
100 %
80 %
60 %
40 %
20 %
0
RR
R-A
R-G
R-F
R-E
Land-cover change

(a)



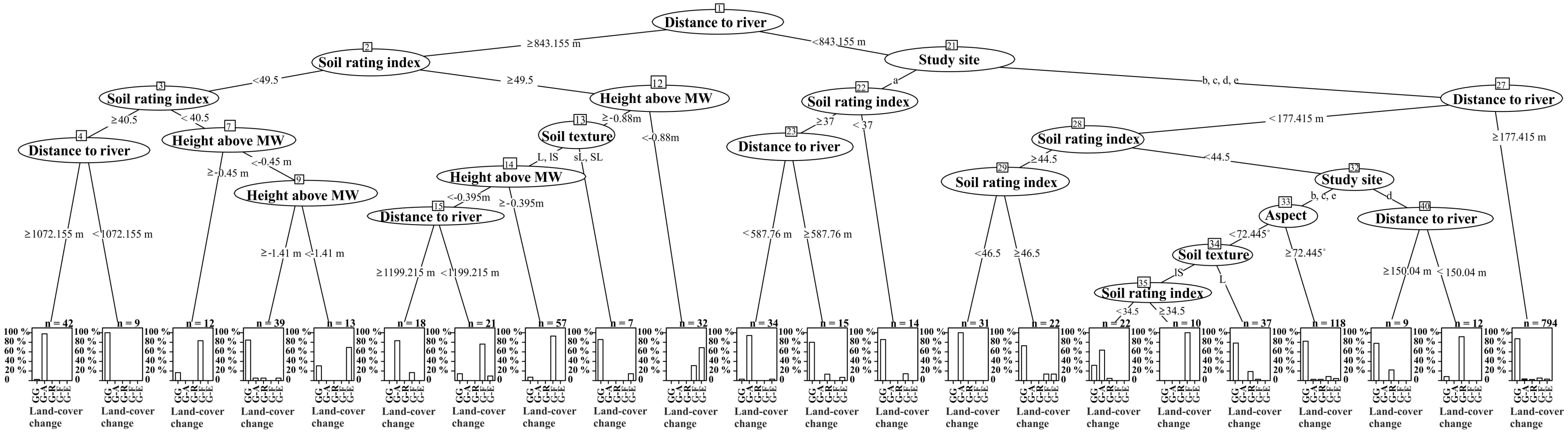
(**b**)

Figure 2-A4. The CART result of riparian forest change and environmental factors (**a**. 1978-1995; **b**. 1995-2010). Abbreviations: RR: stable riparian forest; R-A: riparian forest to arable land; R-G: riparian forest to grassland; R-F: riparian forest to other forests; RE: riparian forest to other land cover; the small letters refer to the study sites, see Fig. 2.1.



1
Study site
a
b, c, d, e
3
Study site
b, c
d, e
4
Height above MW
< 0.325 m
≥0.325 m
5
Distance to river
< 1061.47 m
≥1061.47 m
6
Soil rating index
≥44.5
<44.5
7
Soil rating index
< 48
≥48
9
Distance to river
≥423.88 m
<423.88 m
12
Study site
c
b
13
Soil rating index
≥19.5
<19.5
16
Distance to river
≥417.825 m
<417.825 m
17
Height above MW
≥-1.285 m
<-1.285 m
n = 310
n = 63
n = 73
n = 38
n = 126
n = 17
n = 73
n = 12
n = 194
n = 108
n = 109
n = 349
100 %
80 %
60 %
40 %
20 %
0
GG
G-A
G-R
G-F
G-E
Land-cover change

(a)



(**b**)

Figure 2-A5. The CART result of grassland change and environmental factors ((**a**) 1978-1995; (**b**) 1995-2010). Abbreviations: GG: stable grassland; G-A: grassland to arable land; G-R: grassland to riparian forest; G-F: grassland to other forests; G-E: grassland to other land cover; S: sand; Sl & lS: loamy sand; SL: very loamy sand; sL: sandy loam; L: loam; MoL: moor/ loam, soil consisting of peat and loam; the small letters refer to the study sites, see Fig. 2.1.

Table 3-A1. List of selected hydrological parameters.

Tabelle 3-A1. Liste ausgewählter hydrologischer Parameter.

Variables	**Units**	**Descriptions**	**Data Source**
FD	d/a	Mean flooding duration (1999–2008)	BfG
GWFA_Flu	cm	Depth to groundwater: mean water minus mean low water (mean annual value, 1999–2008)	RMD
V-HQ5	m/s	Flow velocity of a five-year flood	BAW
Height_MW	m	Height relative to the mean water level	BfG (MW)
Dist_Danube	m	Distance to the Danube River	
Dist_WB	m	Distance to the nearest water body	

Table 3-A2. Classification of land-cover into five types and 21 subtypes.

Tabelle 3-A2. Klassifizierung der Landbedeckung in fünf Typen und 21 Untertypen.

Types	**Subtypes**	**Descriptions**
Woody vegetation	Forest	A complex of trees and other woody vegetation
	Copse	A thicket of trees or shrubs
Agricultural land	Arable land	Land where crops such as maize, wheat, and rye are sown
	Grassland	Grass-dominated land mown for fodder production or grazed
	Orchard	Garden with fruit trees close to settlements
Water body	Artificial pond	A gravel pit for extraction of gravel, filled with water
	Backwater	A water body periodically or seasonally connected to the main channel
	Backwater lake	A stagnant water body close to and not connected to the main channel

	Creek	A small narrow stream
	River	The Danube River
Margin	Field hedge	Dense shrubs and trees in line separating fields from each other
	Field margin	Non-woody vegetation and grass strips in line between fields
	Road hedge	Closely spaced shrubs and trees in line separating roads from adjoining fields or other facilities
	Road margin	Non-woody vegetation and grass strips in line separating road from adjoining fields or other facilities
Built-up land	Vegetated path	Unpaved path covered with vegetation (e.g., in forest, between fields)
	Path	Paved path with concrete or other surfaces
	Railway	Railway for transportation
	Road	Routes with one or more lanes
	Settlements	Houses/homesteads grouped together
	Construction site	Bare land used for construction
	Industrial land	Land used for industrial purposes (e.g., wastewater treatment)

Table 3-A3. Landscape metrics calculated in the 500 m buffer zone (LANG & TIEDE 2003, MCGARIGAL & MARKS 1995).

Tabelle 3-A3. Landschaftsmaße berechnet in der 500 m Pufferzone (LANG & TIEDE 2003, MCGARIGAL & MARKS 1995).

Abbreviations	**Metrics**	**Descriptions**	**Units**	**Scale Levels**
PLAND	Percentage of Landscape	the proportional abundance of each patch type in the landscape	%	Class Level

NP	Number of Patches	the number of patches of the corresponding patch type	None	Class Level
ED	Edge Density	the sum of the lengths of all edge segments in the landscape, divided by the total landscape area	m/ha	Landscape Level
MESH	Effective Mesh Size	the size of patches when the landscape is divided into S areas (each of the same size) with the same degree of landscape division as obtained for the observed cumulative area distribution	ha	Landscape Level
Rich	Richness Index	the number of land cover classes	None	Landscape Level
Domi	Dominance Index	the deviation from maximum diversity	None	Landscape Level
Hemeroby	Landscape Hemeroby Index	area-weighted hemeroby index	None	Landscape Level

Table 3-A4. Assignment of the hemeroby degrees to the land use types in this study.

Tabelle 3-A4. Zuordnung der Hemerobiegrade zu den Landnutzungsarten in dieser Studie.

Degree of Hemeroby*	CLC-Code and CLC-Class of the DLM-DE	Land Cover in this Study
1. Ahemerobic–Almost no human impacts	332 Bare rocks	
	335 Glaciers and perpetual snow	
2. Oligohemerobic–Weak human impacts	311 Broad-leaved forest	Forest
	312 Coniferous forest (PNV)	
	313 Mixed forest (PNV)	
	331 Beaches, dunes, sands	

	411 Inland marshes	
	412 Peat bogs	
	421 Salt marshes	
	423 Intertidal flats	
	521 Coastal lagoons	
	522 Estuaries	
	523 Sea and ocean	
3. Mesohemerobic–Moderate human impacts	312 Coniferous forest (not PNV)	
	313 Mixed forest (not PNV)	
	321 Natural grasslands	
	322 Moors and heathland	
	324 Transitional woodland-shrub	Copse
	333 Sparsely vegetated areas	
	334 Burnt areas	
4. β-Euhemerobic–Moderate-strong human impacts	141 Green urban areas	
	231 Pastures	
	243 Land principally occupied by agriculture, with significant areas of natural vegetation	Grassland
	511 Water courses	River
	512 Water bodies	Artificial pond, Backwater, Backwater lake, Creek
5. α-Euhemerobic–Strong human impacts	142 Sport and leisure facilities	Vegetated path
	211 Non-irrigated arable land	Arable land, Field hedge, Field margin

	221 Vineyards	
	222 Fruit trees and berry plantations	Orchard
	242 Complex cultivation patterns	
6. Polyhemerobic–Very strong human impacts	112 Discontinuous urban fabric	
	131 Mineral extraction sites	
	132 Dump sites	
	133 Construction sites	Construction site
7. Metahemerobic–Excessively strong human impact–Biocoenosis destroyed	111 Continuous urban fabric	Settlements
	121 Industrial or commercial units	Industrial land
	122 Road and rail networks and associated land	Railway, Road, Path, Road hedge, Road margin
	123 Port areas	
	124 Airports	

Table 3-A5. List of selected environmental parameters at the local level.

Tabelle 3-A5. Liste ausgewählter Umweltparameter auf lokaler Ebene.

Group Variables	Variables	Units	Descriptions	Data Source
Soil parameters	Soil_tx	None	Soil texture	LDBV
	Soil_ty	None	Soil type	LDBV
	Sand	%	Sand content in the upper soil	RMD
	Clay	%	Clay content in the upper soil	RMD

	Humus	%	Humus content in the upper soil	RMD
	Carbonate	%	Carbonate content in the upper soil	RMD
	ThLoam	cm	Thickness of loam layer in the profile	RMD
Topographic parameters	Slope	°	Slope	BKG (DEM)
	HLI	None	Heat load index (derived from aspect)	BKG (DEM)
	Dist_road	m	Distance to the nearest road/railway	

Table 3-A6. Constancy table of the ten resulting vegetation clusters in the Danube Floodplain. The most frequent species per cluster are listed in the order of descending overall constancy (%). The significant indicator species (p-value < 0.05) of each cluster (Indicator Value > 25) are marked with superscript (signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05). The p-values were calculated from a Monte Carlo permutation test for each species. Only species with constancy value > 20 % are shown. The constancies of the species belonging to the same diagnostic group are framed. Group1: *Glyceria maxima-Persicaria amphibia* cluster; Group 2: *Phragmites australis-Carex riparia* cluster; Group 3: *Persicaria hydropiper-Rorippa amphibia* cluster; Group 4: *Salix viminalis* cluster; Group 5: *Salix alba* cluster; Group 6: *Agrostis stolonifera-Persicaria maculosa* cluster; Group 7: *Prunus padus* cluster; Group 8: *Alopecurus pratensis-Taraxacum officinale* cluster; Group 9: *Cornus sanguinea-Crataegus monogyna* cluster; Group 10: *Acer pseudoplatanus-Fraxinus excelsior* cluster.

Tabelle 3-A6. Stetigkeitstabelle der zehn Vegetationscluster im Donau-Auengebiet. Die Arten mit der höchsten Stetigkeit pro Cluster sind in der Reihenfolge abnehmender Gesamtstetigkeit (%) aufgelistet. Die signifikanten Indikatorarten (p-Wert < 0,05) jedes Clusters (Indikatorwert > 25) sind mit Signifikanzindikatoren markiert (Signifikanzcodes: 0 '***' 0.001 '**' 0.01 '*' 0.05). Die p-Werte wurden mittels Monte-Carlo-Permutationstest für jede Art berechnet. Es werden nur Arten mit einem Stetigkeitswert von > 20% gezeigt. Die Stetigkeiten der Arten, die zur gleichen Diagnosegruppe gehören, werden umrahmt.

Group 1: *Glyceria maxima-Persicaria amphibia* Cluster; Group 2: *Phragmites australis-Carex riparia* Cluster; Group 3: *Persicaria hydropiper-Rorippa amphibia* Cluster; Group 4: *Salix viminalis* Cluster; Group 5: *Salix alba* Cluster; Group 6: *Agrostis stolonifera-Persicaria maculosa* Cluster; Group 7: *Prunus padus* Cluster; Group 8: *Alopecurus pratensis-Taraxacum officinale* Cluster; Group 9: *Cornus sanguinea-Crataegus monogyna* Cluster; Group 10: *Acer pseudoplatanus-Fraxinus excelsior* Cluster.

Group	**1**	**2**	**3**	**6**	**8**	**4**	**5**	**7**	**9**	**10**
Number of relevés	18	6	4	4	3	20	16	11	20	6
Glyceria maxima	100***	0	25	0	0	0	0	0	0	0
Persicaria amphibia	50**	0	0	0	0	5	0	0	0	0
Rumex crispus	28	0	0	25	0	0	0	0	0	0
Carex disticha	22	0	0	0	0	0	0	0	0	0
Stachys palustris	28	33	0	0	0	10	12	9	0	0
Symphytum officinale	28	33	0	0	0	15	12	18	15	0
Phragmites australis	28	67**	50	0	0	35	31	9	20	0
Iris pseudacorus	17	50	75	0	0	0	12	9	5	0
Carex acuta	67	17	75	0	0	5	0	0	0	0
Galium palustre	33	33	50*	0	0	5	0	27	0	0
Carex riparia	0	33*	0	0	0	0	0	0	0	0
Solidago gigantea	0	33	0	0	0	15	6	0	15	0
Rorippa amphibia	6	0	50**	0	0	0	0	0	0	0
Cyperus fuscus	0	0	25	0	0	0	0	0	0	0
Leersia oryzoides	0	0	25	0	0	0	0	0	0	0
Limosella aquatica	0	0	25	0	0	0	0	0	0	0
Persicaria lapathifolia	0	0	25	0	0	0	0	0	0	0
Rumex aquaticus	0	0	25	0	0	0	0	0	0	0
Rumex palustris	0	0	25	0	0	0	0	0	0	0
Scirpus radicans	0	0	25	0	0	0	0	0	0	0
Persicaria hydropiper	0	0	75**	25	0	10	6	0	0	0
Persicaria dubia	22	17	50	25	0	20	0	0	0	0
Rorippa palustris	39	0	50*	25	0	15	0	0	0	0
Myosotis scorpioides agg.	0	0	50	25	0	5	6	0	0	0
Lythrum salicaria	11	17	25	25	0	15	6	0	0	0
Rorippa anceps	11	0	25	25	0	0	0	0	0	0
Veronica catenata	6	0	25	25	0	0	0	0	0	0
Agrostis stolonifera agg.	0	17	25	100***	0	5	6	18	0	17
Lysimachia nummularia	0	17	25	75	0	15	0	27	10	0
Rorippa sylvestris	6	0	25	50**	0	0	0	0	0	0
Persicaria maculosa	0	0	0	50**	0	0	0	0	0	0
Plantago intermedia	0	0	0	50**	0	0	0	0	0	0
Sanguisorba officinalis	0	0	0	50**	0	0	0	0	0	0
Festuca arundinacea	0	17	0	25	0	0	6	0	5	0
Elymus repens	0	0	0	25	0	0	6	0	0	0
Callitriche palustris agg.	0	17	0	25	0	0	0	0	0	0
Carex hirta	0	0	0	25	0	0	0	0	5	0
Cerastium holosteoides	0	0	0	25	0	0	0	0	0	0
Echinochloa crus.galli	0	0	0	25	0	0	0	0	0	0
Galium album	0	0	0	25	0	0	0	0	0	0
Lolium perenne	0	0	0	25	0	0	0	0	0	0

Plantago major	0	0	0	25	0	0	0	0	0	0
Potentilla anserina	0	0	0	25	0	0	0	0	0	0
Ranunculus circinatus	0	0	0	25	0	0	0	0	0	0
Potentilla reptans	0	0	0	50	33	0	6	0	5	0
Plantago lanceolata	6	0	0	50	33	0	0	0	0	0
Ranunculus repens	22	0	0	75	100	10	0	0	5	0
Taraxacum officinale	17	17	0	50	100***	5	0	0	10	0
Rumex obtusifolius	6	17	0	75	100	15	0	0	5	0
Alopecurus pratensis	0	0	0	25	100***	0	0	0	0	0
Trifolium repens	0	0	0	25	33	0	0	0	0	0
Dactylis glomerata	0	0	0	0	67**	5	12	27	25	17
Festuca pratensis	0	0	0	0	67***	0	0	0	5	0
Lolium multiflorum	0	0	0	0	67**	0	0	0	0	0
Achillea millefolium agg.	0	0	0	0	33*	5	0	0	0	0
Angelica sylvestris	0	0	0	0	33	0	0	9	5	0
Salix triandra	0	17	25	0	0	60	6	0	0	0
Salix viminalis	0	0	0	0	0	60**	12	0	20	0
Calystegia sepium	6	17	0	0	0	35	12	18	25	0
Solanum dulcamara	6	0	0	0	0	30	6	9	20	0
Salix alba	0	17	0	0	0	10	100***	9	30	0
Acer negundo	0	0	0	0	0	10	31	9	5	0
Arctium lappa	0	0	0	0	0	10	31	9	5	0
Carduus personata	0	0	0	0	0	0	31	27	0	0
Salix rubens	6	0	0	0	0	15	25	0	10	0
Lamium maculatum	0	0	0	0	0	5	25	0	15	17
Impatiens parviflora	0	0	0	0	0	5	19	55	10	33
Valeriana officinalis agg.	6	17	0	0	0	5	6	27	10	0
Sambucus nigra	0	0	0	0	0	30	19	55	40	0
Brachypodium sylvaticum	0	0	0	0	0	0	12	36	40	17
Alnus incana	0	0	0	0	0	5	19	27	20	0
Crataegus monogyna	0	0	0	0	0	0	0	0	35*	17
Acer campestre	0	0	0	0	0	5	6	9	30	0
Viburnum opulus	0	0	0	0	0	5	6	18	30	17
Chaerophyllum bulbosum	0	0	0	0	0	10	19	0	20	0
Rhamnus cathartica	0	0	0	0	0	0	0	18	20	0
Scrophularia nodosa	0	0	0	0	0	10	6	9	20	0
Prunus padus	0	0	0	0	0	5	0	91***	55	50
Festuca gigantea	0	0	0	0	0	10	19	64	20	50
Galeopsis tetrahit agg.	0	0	0	0	0	0	19	45	35	33
Cornus sanguinea	0	0	0	0	0	10	12	55	95***	50
Aegopodium podagraria	0	0	0	0	0	15	12	36	60	50
Alliaria petiolata	0	0	0	0	0	15	12	36	50	33
Geum urbanum	0	0	0	0	0	10	6	27	70	83

Circaea lutetiana	0	0	0	0	0	0	6	64	15	83
Acer pseudoplatanus	0	0	0	0	0	0	6	9	10	83***
Primula elatior	0	0	0	0	0	0	0	27	10	83**
Scilla bifolia	0	0	0	0	0	0	0	0	15	67**
Anemone ranunculoides	0	0	0	0	0	0	0	0	10	67***
Tilia cordata	0	0	0	0	0	0	0	9	5	67***
Ulmus minor agg.	0	0	0	0	0	10	0	9	30	50
Quercus robur	0	0	0	0	0	0	0	36	15	50
Stachys sylvatica	0	0	0	0	0	0	0	0	15	50*
Carex sylvatica	0	0	0	0	0	0	0	0	0	50**
Lamium galeobdolon agg.	0	0	0	0	0	0	0	18	0	50
Milium effusum	0	0	0	0	0	0	0	0	0	50**
Paris quadrifolia	0	0	0	0	0	0	0	9	15	33
Corylus avellana	0	0	0	0	0	0	12	18	10	33
Ranunculus ficaria	0	0	0	0	0	5	0	18	10	33
Anemone nemorosa	0	0	0	0	0	0	0	0	5	33***
Carpinus betulus	0	0	0	0	0	0	0	0	5	33
Viola reichenbachiana	0	0	0	0	0	0	0	0	0	33*
Common species										
Phalaris arundinacea	83	50	100	50	33	45	25	27	35	17
Urtica dioica	67	100	25	50	0	100	88	91	90	33
Rubus caesius	0	0	0	0	0	40	69	73	90	50
Poa trivialis	0	17	0	25	67	25	19	45	70	17
Humulus lupulus	0	17	0	0	0	45	44	45	30	0
Impatiens glandulifera	0	0	0	0	0	50	75	27	30	17
Fraxinus excelsior	0	0	0	0	0	15	31	64	25	100***
Glechoma hederacea	0	0	0	25	0	15	25	82	80	83
Euonymus europaea	0	0	0	0	0	5	25	45	60	33
Galium aparine agg.	0	0	0	0	0	10	25	27	25	17

Table 3-A7. Kruskal-Wallis test of the environmental factors among all vegetation clusters.

Tabelle 3-A7. Kruskal-Wallis-Test der Umweltfaktoren unter allen Vegetationcluster.

	Group 1 (n = 18) ***Glyceria maxima-Persicaria amphibia*** **cluster**	**Group 2 (n = 6)** ***Phragmites australis-Carex riparia*** **cluster**	**Group 3 (n = 4)** ***Persicaria hydropiper-Rorippa amphibia*** **cluster**	**Group 4 (n = 20)** ***Salix viminalis*** **cluster**	**Group 5 (n = 16)** ***Salix alba*** **cluster**	**Group 6 (n = 4)** ***Agrostis stolonifera-Persicaria maculosa*** **cluster**	**Group 7 (n = 11)** ***Prunus padus*** **cluster**	**Group 8 (n = 3)** ***Alopecurus pratensis-Taraxacum officinale*** **cluster**	**Group 9 (n = 20)** ***Cornus sanguinea-Crataegus monogyna*** **cluster**	**Group 10 (n = 6)** ***Acer pseudoplatanus-Fraxinus excelsior*** **cluster**
FD (d/a) (p-value = 2.728e-06)***										
Median	67	65	130.5	28.5	23.5	23	13	9	9	13
Range	16–143	9–160	8–161	3–148	6–148	5–185	5–25	4–17	2–37	2–33
GWFA_Flu (cm) (p-value = 0.01669)*										
Median	143	142.5	134	151.5	152	155	139	159	145.5	125
Range	74–189	102–158	129–149	123–189	87–229	136–176	85–169	158–176	114–170	80–142
V_HQ5 (m/s) (p-value = 0.001054)**										
Median	0.38	0.16	0.24	0.31	0.19	0.43	0.16	0.35	0.2	0.13
Range	0.00–0.84	0.03–0.44	0.22–0.29	0.08–0.65	0.00–0.56	0.35–0.89	0.06–0.26	0.18–0.46	0.00–0.68	0.04–0.45
Height_MW (m) (p-value = 0.02343)*										
Median	0.84	1.08	0.95	1.57	1.28	1.97	1.95	1.95	1.65	1.96

Range	-0.26–2.39	-0.34–1.93	0.01–4.17	-0.16–6.2	-0.12–2.32	0.42–4.4	1.21–2.24	1.76–2.12	0.22–2.61	1.22–2.21
ThLoam (cm) (p-value = 0.004905)**										
Median	169	268	123.5	180	181	170	211	417	313	260
Range	27–507	118–488	0–305	69–445	35–439	132–262	0–369	341–505	81–601	2–389
Dist_Danube (m) (p-value = 0.003924)**										
Median	159.3	157.2	56.6	47.7	49.4	66.6	105.8	86.0	88.4	365.6
Range	45.8–777.1	25.1–613.1	29.6–284.7	4.9–328.9	13.2–270.8	6.7–81.8	24.4–504.9	74.6–274.7	5.7–499.5	219.6–759.4
Hemeroby_L (p-value = 0.000706)***										
Median	4.27	3.88	4.24	4.36	4.27	4.05	3.30	4.55	4.02	3.13
Range	2.88–4.89	3.22–4.35	3.23–4.46	3.27–4.92	2.99–4.64	3.95–4.48	2.74–4.60	4.38–4.62	2.93–4.61	2.85–4.34
PLAND_agr (%) (p-value = 6.12e-06)***										
Median	67.415	36.075	51.64	54.265	52.62	50.45	30.06	64.06	51.235	31.525
Range	30.67–88.87	29.64–56.28	33.21–57.32	30.26–76.12	15.73–64.83	32.36–61.43	15.77–41.53	42.47–75.77	24.41–64.11	22.84–67.45
Domi_L (p-value = 0.006429)**										
Median	0.99	0.76	0.79	0.85	0.85	0.8	0.85	0.94	0.81	1.17
Range	0.56–1.53	0.72–1	0.54–0.91	0.54–1.09	0.66–1.13	0.66–0.84	0.49–1.28	0.8–1.09	0.54–1.37	0.8–1.39

Table 3-A8. Habitat characteristics for the vegetation clusters from the landscape level to the local level (Note: Soil texture: G/S/Si = gravel/sand/silt, Gs = sandy gravel, S/Si = sand/silt, L = loam, A = mixed soil texture with wide grain size spectrum (e.g., gravel, silt, clay) ; Soil type: GG = gleysols, BB-GG = cambisols- gleysols, GGa = gleyic fluvisols, AB = fluvic cambisols, AZ = calcaric fluvisols, GG-AZ = gleysols-calcaric fluvisols (SCHACHTSCHABEL et al. 1976).

Tabelle 3-A8. Habitatmerkmale für die Vegetationcluster von der Landschaftsebene bis zur lokalen Ebene (Anmerkung: Bodenart: G/S/Si = Kies/Sand/Schluff, Gs = sandige Kies, S/Si = Sand/Schluff, L = Lehm, A = weites Korngrößenspektrum (z. B. Kies, Schluff, Ton); Bodentyp: GG = Gley, BB-GG = Braunerde-Gley, GGa = Auengley, AB = Vega, AZ = Kalkpaternia, GG-AZ = Gley-Kalkpaternia (SCHACHTSCHABEL et al. 1976).

	Landscape level					**500m buffer zone**				**Local level**						
	Mean flooding duration	**Flow velocity of a five-year flood**	**Distance to the Danube**	**Height relative to the mean water level**	**Depth to groundwater**	**Dominant land use type**	**Landscape heterogeneity**	**Fragmentation caused by infrastructure**	**Landscape hemeroby**	**Site land use**	**Soil texture**	**Soil type**	**Loam content**	**Slope**	**Structural characteristics**	**Supplements**
Group1 ***Glyceria maxima-Persicaria amphibia*** **cluster**	long	high	various distances	low	close	grassland(12/18), arable land (4/18), forest (2/18)	strong heterogeneity	little to medium fragmentation	medium to high hemeroby (2.88–4.89)	grassland	G/S/Si (8/18), S/Si (6/18), A(4/18)	GGa (8/18), AB (6/18), GG-AZ (4/18)	various thickness (38–507 cm)	flat to gentle slope	mostly aggregated (16/18)	some are next to backwater, pond, creek or backwater lake, small depression

Group2 ***Phragmites australis-Carex riparia*** **cluster**	long	low	various distances	low	close	arable land(2/6), grassland(2/6) or forest(2/6)	strong heterogeneity	medium to strong	medium hemeroby (3.22–4.35)	grassland (4/6) or forest (2/6)	G/S/Si(4/6), A(2/6)	GGa (4/6), GG-AZ (2/6)	thick (118–488 cm)	flat to gentle slope	all aggregated	close to pond, backwater, old arm (4/6)
Group3 ***Persicaria hydropiper-Rorippa amphibia*** **cluster**	long	low	close	various heights	close, large fluctuation	arable land(2/4), grassland(1/4), forest(1/4)	strong heterogeneity	strong fragmentation	high hemeroby (3.23–4.46)	grassland	G/S/Si(2/4), A(2/4)	GGa (2/4), GG-AZ (2/4)	various thickness (0–305 cm)	gentle slope	mostly aggregated(3/4)	next to or close to the backwater
Group4 ***Salix viminalis*** **cluster**	long	medium	close	various heights	medium depth, large fluctuation	arable land(11/20), grassland(7/20),settlements(1/20), forest(1/20)	strong heterogeneity	strong fragmentation	high hemeroby (3.27–4.92)	forest (18/20) or grassland(2/20)	A(9/20), G/S/Si(7/20), S/Si(3/20)	GG-AZ (9/20), GGa (7/20), AB (3/20)	various thickness (69–445 cm)	flat to medium slope	mostly aggregated(16/20)	close to river or backwater or backwater lake, slight or medium slope
Group5 ***Salix alba*** **cluster**	long	low	close	low	medium depth	arable land(8/16), grassland(5/16), forest(2/16), industrial land(1/16)	strong heterogeneity	strong fragmentation	medium to high hemeroby (2.99–4.64)	forest	G/S/Si (7/16), A(6/16)	GGa (7/16), GG-AZ (6/16)	various thickness (35–439 cm)	flat to medium slope	mostly aggregated (13/16)	close to vegetated path (5/16), river or backwater

Group6 ***Agrostis stolonifera-Persicaria maculosa*** **cluster**	long	high	close	medium to high	medium depth, large fluctuation	arable land(2/4), forest(1/4), grassland(1/4)	medium heterogeneity	medium fragmentation	high hemeroby (3.95–4.48)	grassland	A(3/4), Gs(1/4)	GG-AZ (3/4), AZ (1/4)	thick (132–262 cm)	flat to gentle slope	mostly aggregated (3/4)	close to the vegetated path and close to river(1/4)
Group7 ***Prunus padus*** **cluster**	short	low	various distances	high	medium to far depth	forest(9/11), grassland(1/11), arable land(1/11)	little heterogeneity	low fragmentation	medium hemeroby (2.74–4.6)	forest	G/S/Si(5/11), A(5/11)	GGa (5/11), GG-AZ (5/11)	various thickness (0–369 cm)	flat to gentle slope	all aggregated	
Group8 ***Alopecurus pratensis-Taraxacum officinale*** **cluster**	short	high	medium	high	far, large fluctuation	arable land(2/3), grassland(1/3)	medium to strong heterogeneity	medium to strong fragmentation	high hemeroby (4.38–4.62)	grassland	A(2/3), G/S/Si (1/3)	GG-AZ(2/3), GGa (1/3)	thick loam layer (341–505 cm)	flat	all aggregated	
Group9 ***Cornus sanguinea-Crataegus monogyna*** **cluster**	short	low	various distances	medium to high	far	arable land (10/20), grassland(6/20), forest(4/20)	little heterogeneity	little fragmentation	medium to high hemeroby (2.93–4.61)	forest	G/S/Si (9/20), A(6/20), S/Si(5/20)	GGa (9/20), GG-AZ (6/20), AB (5/20)	various thickness (81–601 cm)	flat to medium slope	mostly aggregated(17/20)	

Group10 ***Acer pseudoplatanus-Fraxinus excelsior* cluster**	short	low	far	high	medium to far depth	forest (5/6), arable land(1/6)	little heterogeneity	little fragmentation	medium hemeroby (2.85–4.34)	forest	A(4/6), L(2/6)	GG-AZ (4/6), GG+BB-GG (2/6)	various thickness (2–389 cm)	flat to gentle slope	all aggregated	planted(3/6), slight slope (2/6)