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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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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.

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

Erweiterte deutsche Zusammenfassung am Ende des Artikels

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, HÄRDTLE et al. 2006). Vegetation in the floodplain is affected by abiotic (e.g. flooding events) and biotic

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factors (e.g. the life cycle of species, MÜLLER 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 (PETRÁŠOVÁ-ŠIBÍKOVÁ 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, MÜLLER 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, HÄRDTLE et al. 2006, SLEZÁK et al. 2017). Single measures at the landscape level (e.g. edge density) were included in the explanation of floristic gradients (MÉNDEZ-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: (1) How are plant species composition, landscape pattern, and environmental variables related in the Danube Floodplain? (a) How are the hydrological parameters related to species composition? (b) How are the landscape structural parameters related to species composition? (c) How are the site-specific parameters related to species composition? (2) In floodplains under strong human influences, where are the habitats for vegetation types located?

2. Material and Methods

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. 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).

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, b).

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).

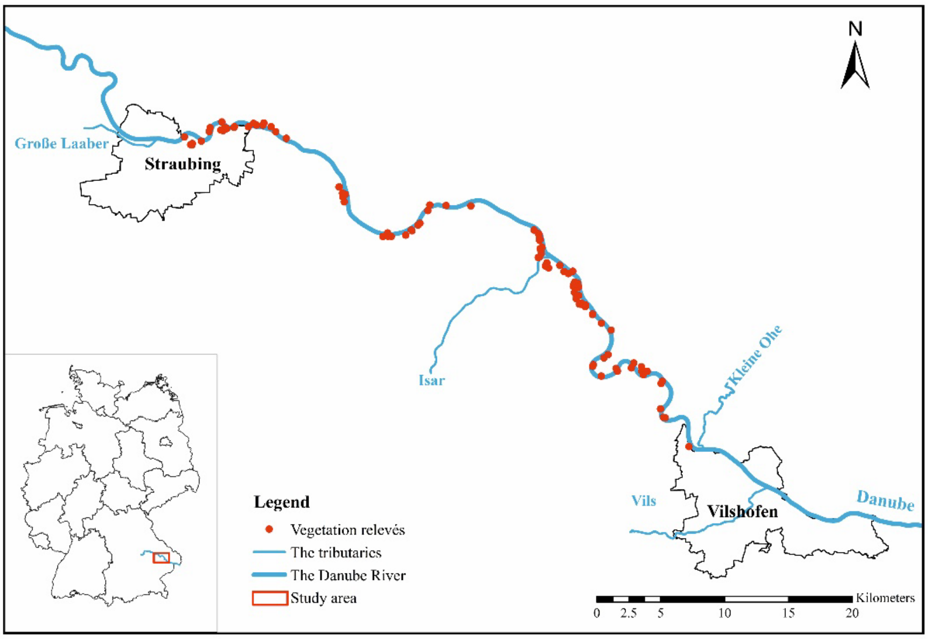

Fig. 1. Locations of vegetation relevés between Straubing and Vilshofen along the Upper Danube. Source: Germany map: VG250 (Administrative boundaries 1: 250,000), provided by the Federal Agency for Cartography and Geodesy (BKG 2007); Vegetation relevés: data collected in the context of "Variantenunabhängige 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. 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).

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. 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 Figure 2.

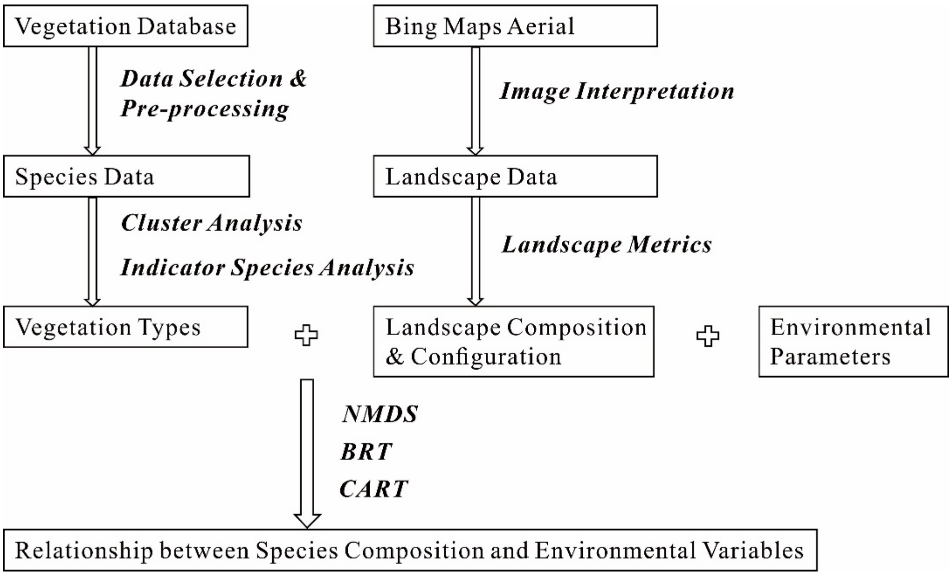

Fig. 2. The workflow of the study.

Abb. 2. Der Arbeitsablauf der Studie.

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 (p) 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 CÁCERES & LEGENDRE 2009). A threshold level of indicator value 25 with 95% significance ($p \leq 0.05$) was set for identifying indicator species. The indicator species were used to characterize and name the vegetation types.

2.4 Analysis of environmental data

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; Supplement E1). 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.

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 (Supplement E2).

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 (Supplement E3). 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, Supplement E4).

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 (Supplement E5). 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):

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).

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 1) was a subset of the multiple variables estimated for each relevé (for the original list, see Supplement E1–E3).

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).

Table 1. Environmental parameters included in the NMDS fitting.

Tabelle 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

3. Results

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 (Supplement S1). The MRPP test validated the number of clusters, with more homogeneity within groups than expected by chance (A = 0.2371, $p = 0.001$).

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.

3.2 Relationship between environmental variables and species composition

In the NMDS (Fig. 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 2). Height_MW is positively correlated to the 2nd axis (Table 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).

Table 2. Significant environmental variables fitted by the NMDS (Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05).

Tabelle 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*

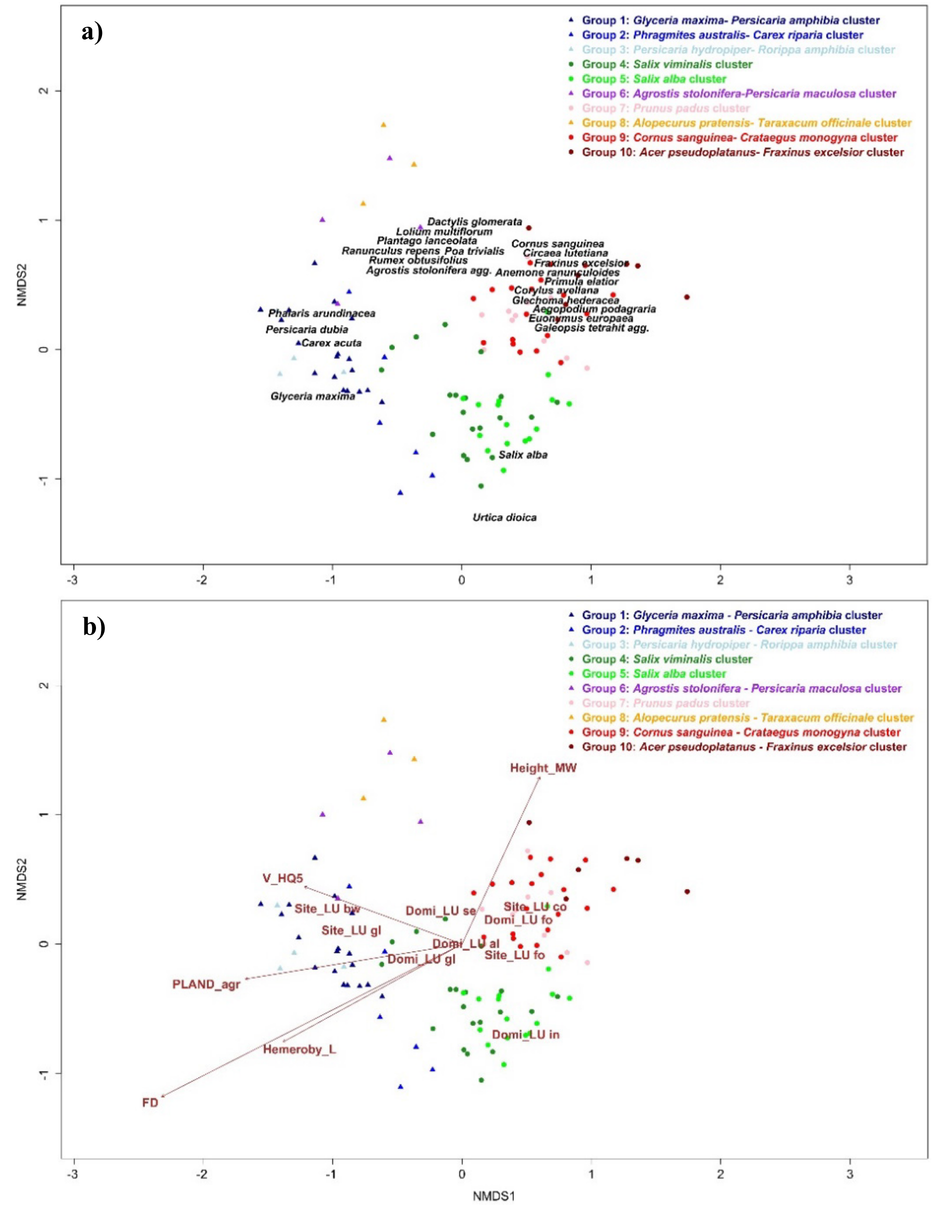

Fig. 3. Non-Metric Multidimensional Scaling (NMDS) with fitted environmental variables and most frequent species. Graphs **a)** and **b)** display axes 1 and 2, while **c)** and **d)** display axes 1 and 3. The brown vectors in **a)** and **c)** show the direction of linear correlation of continuous variables with ordination scores ($p \leq 0.05$). The brown dots in **a)** and **c)** stand for categorical variables ($p \leq 0.05$). Graphs **b)** and **d)** show the most frequent species ($p \leq 0.001$). 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 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.

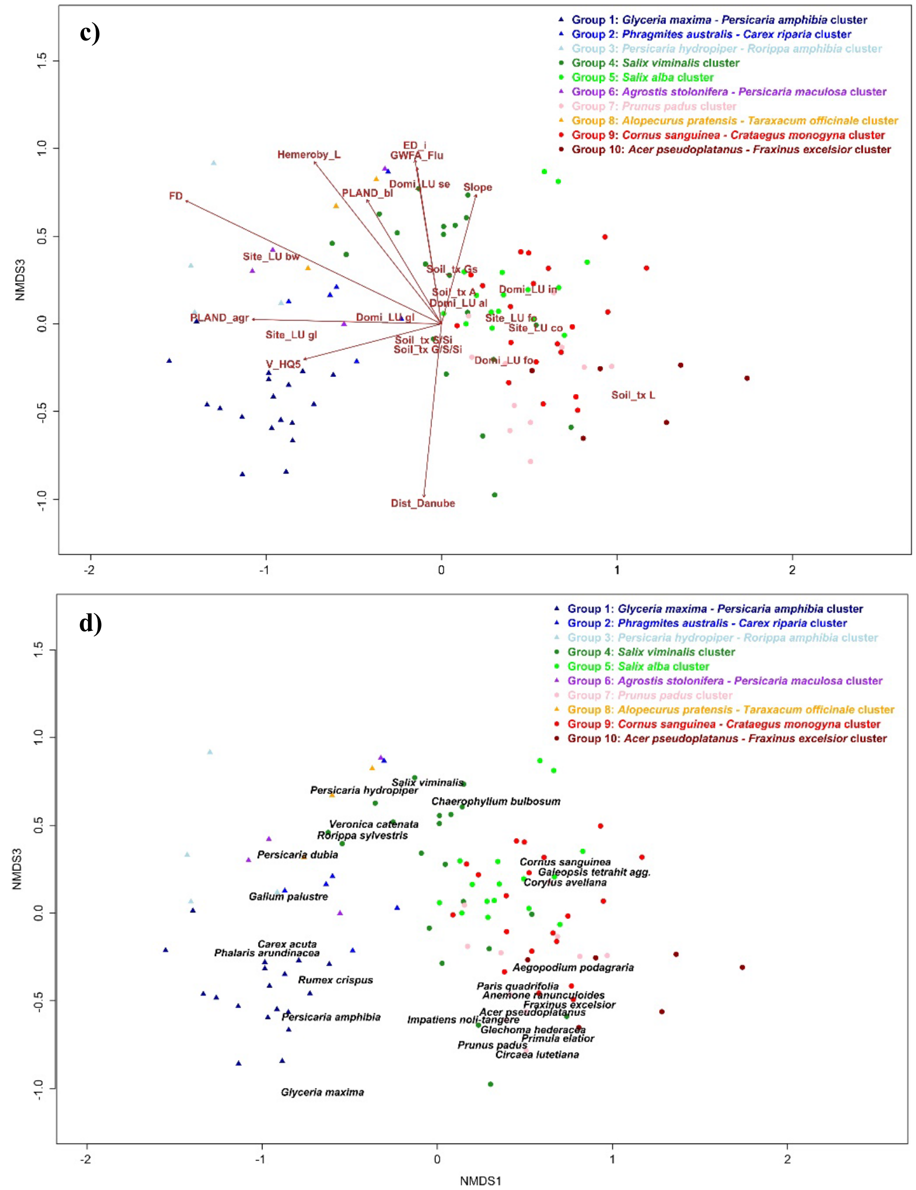

Abb. 3. Non-Metric Multidimensional Scaling (NMDS) mit angepassten Umweltvektoren und häufigsten Arten. **a)** und **b)** zeigen die Achsen 1 und 2 an, während **c)** und **d)** die Achsen 1 und 3 anzeigen. Die braunen Vektoren in **a)** und **c)** zeigen die Richtung der linearen Korrelation kontinuierlicher Umweltvariablen mit den Ordinationsachsen ($p \leq 0{,}05$). Die braunen Punkte in **a)** und **c)** stehen für die kategorialen Umweltvariablen ($p \leq 0{,}05$). **b)** und **d)** zeigen die häufigsten Arten ($p \leq 0{,}001$). 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 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. The relative contributions (%) of environmental variables for the three NMDS ordination axes in the BRT model (abbreviations are explained in Table 1).

Tabelle 3. Die relativen Beiträge (%) der Umweltvariablen für die drei NMDS-Ordinationsachsen im BRT-Modell (Abkürzungen sind in Tab. 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%

Thirteen variables are significantly related to the axes ($p \leq 0.05$, Table 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). 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.

3.3 Habitat characteristics of vegetation types and the CART results

The habitat characteristics as defined by the results from the Kruskal-Wallis test (Supplement E6) and the NMDS are described in detail in Supplement E7.

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 4, Fig.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.

Table 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 1.)

Tabelle 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 s. Tab. 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

4. Discussion

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

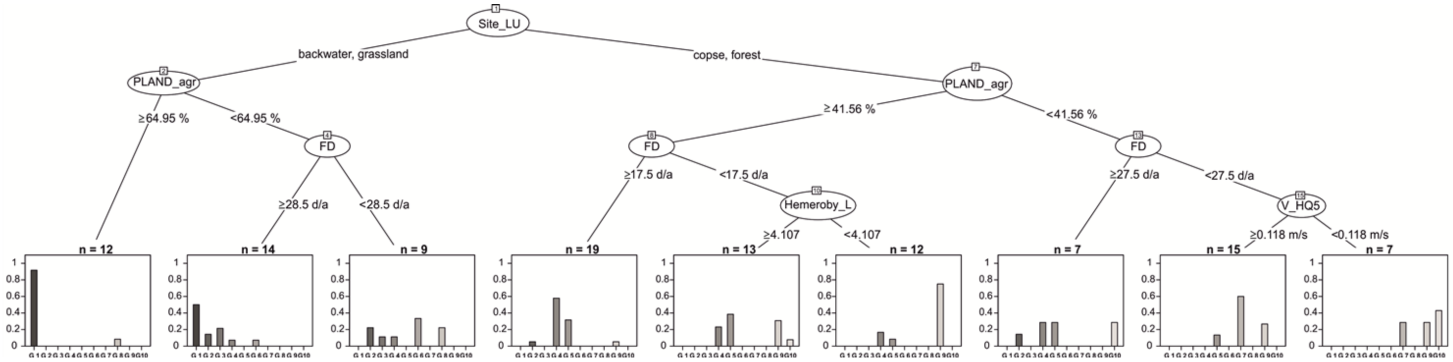

Fig. 4. The CART results of vegetation types and environmental factors. Abbreviations: G1: the *Glyceria maxima-Persicaria amphibia* cluster; G2: the *Phragmites australis-Carex riparia* cluster; G3: the *Persicaria hydropiper-Rorippa amphibia* cluster; G4: the *Salix viminalis* cluster; G5: the *Salix 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 1.

Abb. 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 1.

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.

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, Šálek 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).

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.

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 (Supplement E7). 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 (MÜLLER 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 (MÜLLER 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.

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) aus der Wald- und Offenlandvegetation identifiziert, welche das hydrologische Gefälle in der Aue widerspiegeln.

Dreizehn Variablen standen signifikant mit der Artenzusammensetzung in Beziehung (Tab. 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. 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.

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Author contribution statement

Fang Xu, Sarah Harvolk-Schöning, Peter J. Horchler, Kristin Ludewig and Annette Otte conceived and designed this study. Fang Xu analyzed the data and wrote the paper. Sarah Harvolk-Schöning, Peter J. Horchler, Kristin Ludewig and Annette Otte revised the paper. All authors read and approved the final manuscript.

Supplements

Supplement S1. Constancy table of the ten resulting vegetation clusters in the Danube Floodplain.

Beilage S1. Stetigkeitstabelle der zehn Vegetationscluster im Donau-Auengebiet.

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. List of selected hydrological parameters.

Anhang E1. Liste ausgewählter hydrologischer Parameter.

Supplement E2. Classification of land-cover into five types and 21 subtypes.

Anhang E2. Klassifizierung der Landbedeckung in fünf Typen und 21 Untertypen.

Supplement E3. Landscape metrics calculated in the 500 m buffer zone (LANG & TIEDE 2003, MCGARIGAL & MARKS 1995).

Anhang E3. Landschaftsmaße berechnet in der 500 m Pufferzone (LANG & TIEDE 2003, MCGARIGAL & MARKS 1995).

Supplement E4. Assignment of the hemeroby degrees to the land use types in this study.

Anhang E4. Zuordnung der Hemerobiegrade zu den Landnutzungsarten in dieser Studie.

Supplement E5. List of selected environmental parameters at the local level.

Anhang E5. Liste ausgewählter Umweltparameter auf lokaler Ebene.

Supplement E6. Kruskal-Wallis test of the environmental factors among all vegetation clusters.

Anhang E6. Kruskal-Wallis-Test der Umweltfaktoren unter allen Vegetationcluster.

Supplement E7. Habitat characteristics for the vegetation clusters from the landscape level to the local level.

Anhang E7. Habitatmerkmale für die Vegetationcluster von der Landschaftsebene bis zur lokalen Ebene.

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Supplement S1. 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.

Beilage S1. 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 Steitigkeitswert von > 20% gezeigt. Die Stetigkeiten der Arten, die zur gleichen Diagnosegruppe gehören, sind 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 ***	.	25	.	.	.	.	.	.	.
Persicaria amphibia	50 **	.	.	.	.	5	.	.	.	.
Rumex crispus	28	.	.	25	.	.	.	.	.	.
Carex disticha	22	.	.	.	.	.	.	.	.	.
Stachys palustris	28	33	.	.	.	10	12	9	.	.
Symphytum officinale	28	33	.	.	.	15	12	18	15	.
Phragmites australis	28	67 **	50	.	.	35	31	9	20	.
Iris pseudacorus	17	50	75	.	.	.	12	9	5	.
Carex acuta	67	17	75	.	.	5	.	.	.	.
Galium palustre	33	33	50 *	.	.	5	.	27	.	.
Carex riparia	.	33 *	.	.	.	.	.	.	.	.
Solidago gigantea	.	33	.	.	.	15	6	.	15	.
Rorippa amphibia	6	.	50 **	.	.	.	.	.	.	.
Cyperus fuscus	.	.	25	.	.	.	.	.	.	.
Leersia oryzoides	.	.	25	.	.	.	.	.	.	.
Limosella aquatica	.	.	25	.	.	.	.	.	.	.
Persicaria lapathifolia	.	.	25	.	.	.	.	.	.	.
Rumex aquaticus	.	.	25	.	.	.	.	.	.	.
Rumex palustris	.	.	25	.	.	.	.	.	.	.
Scirpus radicans	.	.	25	.	.	.	.	.	.	.
Persicaria hydropiper	.	.	75 **	25	.	10	6	.	.	.
Persicaria dubia	22	17	50	25	.	20	.	.	.	.
Rorippa palustris	39	.	50 *	25	.	15	.	.	.	.
Myosotis scorpioides agg.	.	.	50	25	.	5	6	.	.	.
Lythrum salicaria	11	17	25	25	.	15	6	.	.	.
Rorippa anceps	11	.	25	25	.	.	.	.	.	.
Veronica catenata	6	.	25	25	.	.	.	.	.	.
Agrostis stolonifera agg.	.	17	25	100 ***	.	5	6	18	.	17
Lysimachia nummularia	.	17	25	75	.	15	.	27	10	.
Rorippa sylvestris	6	.	25	50 **	.	.	.	.	.	.
Persicaria maculosa	.	.	.	50 **	.	.	.	.	.	.
Plantago intermedia	.	.	.	50 **	.	.	.	.	.	.
Sanguisorba officinalis	.	.	.	50 **	.	.	.	.	.	.
Festuca arundinacea	.	17	.	25	.	.	6	.	5	.
Elymus repens	.	.	.	25	.	.	6	.	.	.
Callitriche palustris agg.	.	17	.	25	.	.	.	.	.	.
Carex hirta	.	.	.	25	.	.	.	.	5	.
Cerastium holosteoides	.	.	.	25	.	.	.	.	.	.
Echinochloa crus.galli	.	.	.	25	.	.	.	.	.	.
Galium album	.	.	.	25	.	.	.	.	.	.
Lolium perenne	.	.	.	25	.	.	.	.	.	.
Plantago major	.	.	.	25	.	.	.	.	.	.
Potentilla anserina	.	.	.	25	.	.	.	.	.	.
Ranunculus circinatus	.	.	.	25	.	.	.	.	.	.
Potentilla reptans	.	.	.	50	33	.	6	.	5	.
Plantago lanceolata	6	.	.	50	33	.	.	.	.	.
Ranunculus repens	22	.	.	75	100	10	.	.	5	.
Taraxacum officinale	17	17	.	50	100 ***	5	.	.	10	.
Rumex obtusifolius	6	17	.	75	100	15	.	.	5	.
Alopecurus pratensis	.	.	.	25	100 ***	.	.	.	.	.
Trifolium repens	.	.	.	25	33	.	.	.	.	.
Dactylis glomerata	.	.	.	.	67 **	5	12	27	25	17
Festuca pratensis	.	.	.	.	67 ***	.	.	.	5	.
Lolium multiflorum	.	.	.	.	67 **	.	.	.	.	.
Achillea millefolium agg.	.	.	.	.	33 *	5	.	.	.	.
Angelica sylvestris	.	.	.	.	33	.	.	9	5	.
Salix triandra	.	17	25	.	.	60	6	.	.	.
Salix viminalis	.	.	.	.	.	60 **	12	.	20	.
Calystegia sepium	6	17	.	.	.	35	12	18	25	.
Solanum dulcamara	6	.	.	.	.	30	6	9	20	.
Salix alba	.	17	.	.	.	10	100 ***	9	30	.
Acer negundo	.	.	.	.	.	10	31	9	5	.
Arctium lappa	.	.	.	.	.	10	31	9	5	.
Carduus personata	.	.	.	.	.	.	31	27	.	.
Salix rubens	6	.	.	.	.	15	25	.	10	.
Lamium maculatum	.	.	.	.	.	5	25	.	15	17
Impatiens parviflora	.	.	.	.	.	5	19	55	10	33
Valeriana officinalis agg.	6	17	.	.	.	5	6	27	10	.
Sambucus nigra	.	.	.	.	.	30	19	55	40	.
Brachypodium sylvaticum	.	.	.	.	.	.	12	36	40	17
Alnus incana	.	.	.	.	.	5	19	27	20	.
Crataegus monogyna	.	.	.	.	.	.	.	.	35 *	17
Acer campestre	.	.	.	.	.	5	6	9	30	.
Viburnum opulus	.	.	.	.	.	5	6	18	30	17
Chaerophyllum bulbosum	.	.	.	.	.	10	19	.	20	.
Rhamnus cathartica	.	.	.	.	.	.	.	18	20	.
Scrophularia nodosa	.	.	.	.	.	10	6	9	20	.
Prunus padus	.	.	.	.	.	5	.	91 ***	55	50
Festuca gigantea	.	.	.	.	.	10	19	64	20	50
Galeopsis tetrahit agg.	.	.	.	.	.	.	19	45	35	33
Cornus sanguinea	.	.	.	.	.	10	12	55	95 ***	50
Aegopodium podagraria	.	.	.	.	.	15	12	36	60	50
Alliaria petiolata	.	.	.	.	.	15	12	36	50	33
Geum urbanum	.	.	.	.	.	10	6	27	70	83
Circaea lutetiana	.	.	.	.	.	.	6	64	15	83
Acer pseudoplatanus	.	.	.	.	.	.	6	9	10	83 ***
Primula elatior	.	.	.	.	.	.	.	27	10	83 **
Scilla bifolia	.	.	.	.	.	.	.	.	15	67 **
Anemone ranunculoides	.	.	.	.	.	.	.	.	10	67 ***
Tilia cordata	.	.	.	.	.	.	.	9	5	67 ***
Ulmus minor agg.	.	.	.	.	.	10	.	9	30	50
Quercus robur	.	.	.	.	.	.	.	36	15	50
Stachys sylvatica	.	.	.	.	.	.	.	.	15	50 *
Carex sylvatica	.	.	.	.	.	.	.	.	.	50 **
Lamium galeobdolon agg.	.	.	.	.	.	.	.	18	.	50
Milium effusum	.	.	.	.	.	.	.	.	.	50 **
Paris quadrifolia	.	.	.	.	.	.	.	9	15	33
Corylus avellana	.	.	.	.	.	.	12	18	10	33
Ranunculus ficaria	.	.	.	.	.	5	.	18	10	33
Anemone nemorosa	.	.	.	.	.	.	.	.	5	33 ***
Carpinus betulus	.	.	.	.	.	.	.	.	5	33
Viola reichenbachiana	.	.	.	.	.	.	.	.	.	33 *
Common species										
Phalaris arundinacea	83	50	100	50	33	45	25	27	35	17
Urtica dioica	67	100	25	50	.	100	88	91	90	33
Rubus caesius	.	.	.	.	.	40	69	73	90	50
Poa trivialis	.	17	.	25	67	25	19	45	70	17
Humulus lupulus	.	17	.	.	.	45	44	45	30	.
Impatiens glandulifera	.	.	.	.	.	50	75	27	30	17
Fraxinus excelsior	.	.	.	.	.	15	31	64	25	100 ***
Glechoma hederacea	.	.	.	25	.	15	25	82	80	83
Euonymus europaea	.	.	.	.	.	5	25	45	60	33
Galium aparine agg.	.	.	.	.	.	10	25	27	25	17

Xu et al.: Distribution pattern of floodplain vegetation remnants along the Danube River

Supplement E1. List of selected hydrological parameters.

Anhang E1. 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	

Supplement E2. Classification of land-cover into five types and 21 subtypes.

Anhang E2. 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)

Supplement E3. Landscape metrics calculated in the 500 m buffer zone (LANG & TIEDE 2003, MCGARIGAL & MARKS 1995).

Anhang E3. 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

Supplement E4. Assignment of the hemeroby degrees to the land use types in this study.

Anhang E4. 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 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	

Supplement E5. List of selected environmental parameters at the local level.

Anhang E5. 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	

Supplement E6. Kruskal-Wallis test of the environmental factors among all vegetation clusters.

Anhang E6. 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

Supplement E7. 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).

Anhang E7. 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 ground-water**	**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 pseudo-platanus-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)