



universität
wien

MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

„Effects of structural heterogeneity of floodplain forests
and hydrological dynamic on bird assemblages: a case
study from the Donau-Auen National Park
(Eastern Austria)“

verfasst von / submitted by

Lilith Adrion, BSc

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of
Master of Science (MSc)

Wien, 2016 / Vienna 2016

Studienkennzahl lt. Studienblatt /
degree programme code as it appears on
the student record sheet:

A 066879

Studienrichtung lt. Studienblatt /
degree programme as it appears on
the student record sheet:

Masterstudium
Naturschutz und Biodiversitätsmanagement

Betreut von / Supervisor:

Ass.-Prof. Dr. Christian H. Schulze

Acknowledgement

I thank my thesis advisor Christian Schulze for his great help. I'm very grateful for the support of the National Park Donau-Auen and thank especially Karoline Zsak and Christian Baumgartner. For the provision of the data of the forest inventory I thank the Österreichische Bundesforste AG and the MA 49, namely Robert Zeiner and Monika Kanzian (ÖBF) and Werner Fleck and Alexander Faltjek (MA 49). For her contribution of data (dead wood volume and forest structure elements) but above all her support at all times I want to thank Barbara Waringer. Also I thank Barbara Hönigsberger for the contribution of the canopy height data. I would also like to thank Elisabeth Knapp and Rachel Firkins for their support at any given time. I'm infinitely grateful for the love and support of my husband Marius Adrion. Without you I still would be stuck in the deepest copse I've ever endured (figuratively and literally).

Last but not least I thank my parents Ute and Klaus Jopp for everything.

Abstract

Bird assemblages are influenced by forest structure and landscape elements, which are very diverse in highly productive riparian forests. In this study the influence of those elements on the bird assemblage of the National Park Donau-Auen is examined. In spring 2015 the bird assemblage was surveyed three times with 5-minute point counts in 72 randomly chosen forest plots. The bird richness was higher closer to permanent water bodies. The proportion of alder in the canopy had a positive effect on bird richness and diversity. The proportion of white poplar affected the bird diversity negatively and so did the dead wood volume. These results can be explained by a positive effect of soil moisture, and a better food supply due to emerging adult aquatic insects closer to permanent water bodies. In the National Park Donau-Auen, dead wood volume may indicate former forestry sites, with low structural diversity and therefore little attraction for birds. Species turnover accounted for 90% of the beta diversity. But no relationship between the bird species composition and the habitat and landscape variables was found. Additionally, the bird species have no distinct habitat preferences. The bird assemblage of the riparian forest seems to remain stable in relation to environmental influences.

Keywords: Danube, riparian landscape, bird species richness, bird species diversity, point counts

Zusammenfassung

Vogelgesellschaften werden von Walstruktur- und Landschaftsmerkmalen, die in hoch produktiven Auwäldern sehr divers ausgeprägt sind, beeinflusst. In der vorliegenden Studie werden diese Einflüsse auf die Vogelgesellschaft des Nationalpark Donau-Auen untersucht. Hierfür wurden in 72 zufällig ausgewählten Waldflächen alle Vogelarten jeweils drei Mal im Frühjahr 2015 mittels 5-Minuten-Punktzählungen erhoben. Der Vogelartenreichtum nahm mit zunehmender Distanz zu Gewässern ab. Der Anteil von Erle in der Baumschicht hat einen positiven Einfluss auf Vogelartenreichtum und -diversität. Der Anteil von Weißpappel in der Baumschicht sowie das Volumen von Totholz haben einen negativen Einfluss auf die Vogelartendiversität. Diese Ergebnisse könnten dadurch erklärt werden, dass Vogelartenreichtum und -diversität auf feuchteren Flächen höher ist; dass das Nahrungsangebot (durch schlüpfende aquatische Fluginsekten) zu Gewässern hin größer wird und dass das Totholzvolumen in den vormals wirtschaftlich genutzten Flächen ein Indikator für einförmige und für Vögel unattraktive Flächen ist. Der Artenwechsel macht 90% der Beta-Diversität aus. Es konnte allerdings kein Zusammenhang zwischen den Habitat- und Landschaftsvariablen und der Vogelartenzusammensetzung gefunden werden. Die Vogelarten zeigen außerdem keine ausgeprägten Habitat Präferenzen. Die Vogelgesellschaft des im Nationalpark geschützten Donau-Auwaldes scheint Umwelteinflüssen gegenüber stabil zu sein.

1. Introduction

The current species composition represents only 2-4 % of the species ever lived (IUCN 2007), the other 96-98% vanished long before human evolution. Extinction is a natural process and happened uncountable times during evolution (Tepper 2010). There is a natural “background” extinction, which is counterbalanced by species origination (IUCN 2007, McCallum 2015). At least 5 mass extinctions in the geological past (Ordovician, Devonian, Permian, Triassic and Cretaceous mass extinction) out-paced origination (McCallum 2015). The current rate of extinction is 1,000-10,000 times higher than the natural background rate (IUCN 2007). Also, the rate of extinction of vertebrates is since 1980 71 to 297 times faster than in the last mass extinction (McCallum 2015). We are right in the middle of the sixth mass extinction and this time only one species is responsible: *Homo sapiens* (McCallum 2015). The International Union for Nature Conservation (IUCN 2007) declares the main reason for worldwide species extinction is the habitat loss through destruction and degradation. Accordingly, one way to stop the extinction is to stop habitat degradation.

In Europe, riverine landscapes are some of the major biodiversity hotspots as well as important corridors for migrating species (Figarski and Kajtoch 2015), but flow regulation and fragmentation of rivers leads to species extinction (Pimm et al. 2014). So the deterioration of riverine habitats can have an effect of catastrophic extent (Figarski and Kajtoch 2015). Already existing modifications of freshwater systems may have harmed species to an extent where no future protection will prevent extinction (Pimm et al. 2014). Nearly 50 % of the rivers in Europe have altered habitats and suffer hydromorphological pressures. This is due to flooding prevention, ship navigation and hydrodynamic power plants. In Austria up to 80 % of the large rivers are at least moderately affected. Water pollution is not the main problem anymore – it is the alteration of free flowing river stretches. Only a third of the length of the major rivers remains free flowing (Fehér et al. 2012). The loss of riparian areas in the last 150 years is drastic. Two thirds of riparian areas at the Danube shore between Passau and Bratislava were lost.

Yet, riparian landscapes are highly productive and diverse ecosystems, linking terrestrial and stream habitats (Iwata et al. 2003). Bird communities are related to diverse habitat elements of the riverscape (Sullivan et al. 2007). According to Hewson et al. (2011) the habitat structure and the floristic species composition of woodland are significantly involved when trying to illuminate the distribution of birds.

Tree species richness, canopy cover and canopy height as well as tree density affect bird species composition and abundances (James and Wamer 1982, Tomialojc and Wesolowski 1994). Canopy height can function as a surrogate for complex habitat structures on small scales like the structure diversity of shrub (e.g. the percentage of bushes; Batáry et al. 2014) and herbal layer, which are particularly important for resource provision. Such micro habitat elements are difficult to quantify and measure (Fuller and Rothery 2013). In general, the more layers a forest has the more vertical structure arises. Complex vertical structure with herbal, shrub and even several tree layers make room for zoological diversity. This is also true for an economically used and selectively cut forest (“Plenterwald”). But those highly stratified forests lack horizontal structure due to forestry management. Particularly tree species diversity and standing and fallen dead wood are reduced (Ellenberg et al. 2010). Fuller and Rothery (2013) and Helle and

Järvinen (1986) state that the forest age has a significant effect on the bird diversity. Normally the older a forest is the more structured it gets (Poulsen 2002). However, bird diversity is not inevitably highest at climax forests, e.g. because they may lack distinct lower layers (Helle and Järvinen 1986). Intermediate disturbance resulting in succession and young forest sites inside an old forest triggers structure diversity (Townsend et al. 1997, Fox 2013) and results in high bird species richness and diversity. This relation applies also for forest edges (Helle and Järvinen 1986, Hagan et al. 1997, Saab 1999). Additionally, mixed forests compose a higher bird diversity than deciduous and coniferous forests (Christen 1983, Mosimann et al. 1987).

This study examines to what extent the structure of riparian forests and the landscape context is affecting bird assemblage in the National Park Donau-Auen, one of the largest remaining floodplain forests in Central Europe. Due to the high hydrological dynamic of floodplain areas forest structure can differ strongly on small spatial scales creating a mosaic of different forest types, certainly contributing significantly to the high diversity of bird assemblages of floodplain forests (Iwata et al. 2003, Sullivan et al. 2007). These forest types are characterized by different dominating tree species, namely alder, ash and white poplar in the case of the floodplain forests east of Vienna, Eastern Austria (Ellenberg et al. 2010). Tree species diversity enhances the diversity of the bird assemblages (Gabbe et al. 2002, Hewson et al. 2011, Fuller and Rothery 2013, Batáry et al. 2014, Munes et al. 2015).

Deadwood represents a habitat variable which proved to affect richness and abundance of bird species (Nilsson 1979, Birčák and Reif 2015, Mag and Ódor 2015). The availability of deadwood in floodplain forests is related to two important factors: the hydrological dynamic contributing to the accumulation of deadwood, and, in the case of the studied floodplain forests along Danube river, former forestry measures. The intensity of forest use is also shaping the age structure of forest areas, as well as the height and the composition and diversity of canopy trees (Bobiec 2002). Old and mature forests are characterized by a greater number of trees that run through a complete life and decomposition cycle, higher number of tree species and more tree size classes. Also, unmanaged forests have more standing and lying dead wood than managed forests (Poulsen 2002). This results in turn in more possibilities for nesting birds and more foraging possibilities. Therefore, I expect that forest age, dead wood volume and height and diversity of canopy layer have a positive influence on the diversity of the bird assemblage, especially in a riparian forest in regard to differences between softwood and hardwood sites (Holmes and Robinson 1981, Buffington et al. 1997).

Additionally, landscape parameters, such as the distance to permanent water bodies and open land, may affect bird assemblages. I expect that the diversity of the bird assemblages increases close to forest periphery structures (e.g. edge of the forest, banks, and hedges). In contrast, the diversity should decrease with the distance to permanent water bodies and open land in general (Rotenberry 1985, Hagan et al. 1997, Hewson et al. 2011). Adult aquatic insects represent an important food source for floodplain forests birds. The abundance of adult aquatic insects emerging from streams decreases with the increasing distance to water (Iwata et al. 2003, Sullivan et al. 2007), followed by a decreasing diversity of the bird assemblages. But bird communities prey also on terrestrial insects feeding on riparian plants (Sullivan et al. 2007), which might counterbalance the effect. Considering all these potential effects, there might be also a difference in bird richness

and species composition between forest sites north and south of the levee protecting the north side against flooding, because the absence of floods north of the dam changes the vegetation and therefore the habitat structure substantially (Ellenberg et al. 2010)

Hence, we particularly address the following hypotheses:

(1) The composition and diversity of bird assemblages of floodplain forests in the Donau-Auen National Park is driven by differences in forest structure shaped by hydrological dynamics and former forestry measures and,

(2) distances to permanent water bodies and open land contribute to differences in composition and diversity of bird assemblages between forest sites.

2. Material and methods

2.1. Study site

The study took place in the National Park Donau-Auen in the federal state Lower Austria north of the river Danube. The study plots were spread between Schönau (48°14' N, 16°61' E) in the west and Stopfenreuth (48°14' N, 16°88' E) in the east (Figure 1) and located north as well as south of the “Marchfeldschutzdamm”, a levee protecting areas north of it against flooding events. The area consists of a network of riparian forest (65%), water bodies (20%) and meadows (15%) (National Park Donau-Auen 2016). The riverine floodplain is characterized by regular flooding, linking aquatic and terrestrial ecosystems, and represents a biodiversity hotspot (Sommerwerk et al. 2009). Since the “training” of the river in the late 19th century the flooding became less frequent, “dead” parts of the river arose and the riverbed deepened (IUCN 2015). The Marchfeldschutzdamm prevents the area north of it from flooding (Margl 1973, Schratt-Ehrendorfer 2011). A disconnection between river and riparian forest impends (IUCN 2015). To work against these problems and to revitalize the Danube an ambitious river restoration project was initialized (IUCN 2015, ViaDonau 2016a). The floodplain forests in the National Park Donau-Auen close to the river and not sealed off by any dam are the most natural and preserved (Brix 1972). They are distinguished by near-natural flooding (regular lateral overflow water with various intensity, fed by events like snowmelt or heavy rain, typically in summer; Tockner and Stanford 2002, Teufelbauer and Frank 2009). After the regulation the dead stream branches and side arms get their water only through groundwater. This rises with flooding but is filtered and nutrient-poor. Additionally the sinking groundwater takes nutrients with it and the soil elutriates (Brix 1972). Nutrient- and sediment-loaded water reaches the wetlands merely through the “Schönauer Schlitz”, an opening to prevent in the dam to prevent breaking (Schratt-Ehrendorfer 2011). The network of floodplains along the rivers Danube and Moravia is one of the last remaining floodplain wetlands in Europe (IUCN 2015) and is as part of the RAMSAR convention on the Austrian list of wetlands of international importance since 1983 (Bundeskanzleramt 1983). In 1996 the “Donau-Auen National Park” was founded (Bundeskanzleramt 1996) and was ratified by the IUCN as a category II national park (IUCN 2015). Parts of the National Park are protected additionally as a Natura 2000 site (since 2007 ratified through Birds Directive and 2011 through the Habitats Directive, Teufelbauer and Frank 2009).

2.2. Study site selection

The surveyed forest sites were selected based on information from the Austrian national forest inventory. The forest inventory is composed of a net of survey points in a hundred-meter grid. For the study sites those points were filtered with ArcMap 10.2 (ESRI). The study sites were situated inside the forest (without a forest margin within a 50m radius) on the northern shore of the Danube river in the federal state Lower Austria and were located at a distance of <100m from a path to be accessible in a reasonable time. To achieve geographical independence the plots were at least 200 m apart from another (Felton et al. 2016). The plots were stratified by distance to next permanent water body using the following categories: <75 m, 75 to <150 m, 150 to <250 m and 250 to <1000 m. For every class initially 25 points were chosen randomly. Excluding points located in close vicinity to nesting sites of Eastern Imperial Eagles and White-tailed Eagles to reduce human disturbance resulted in a total of 72 remaining census point used in this study.

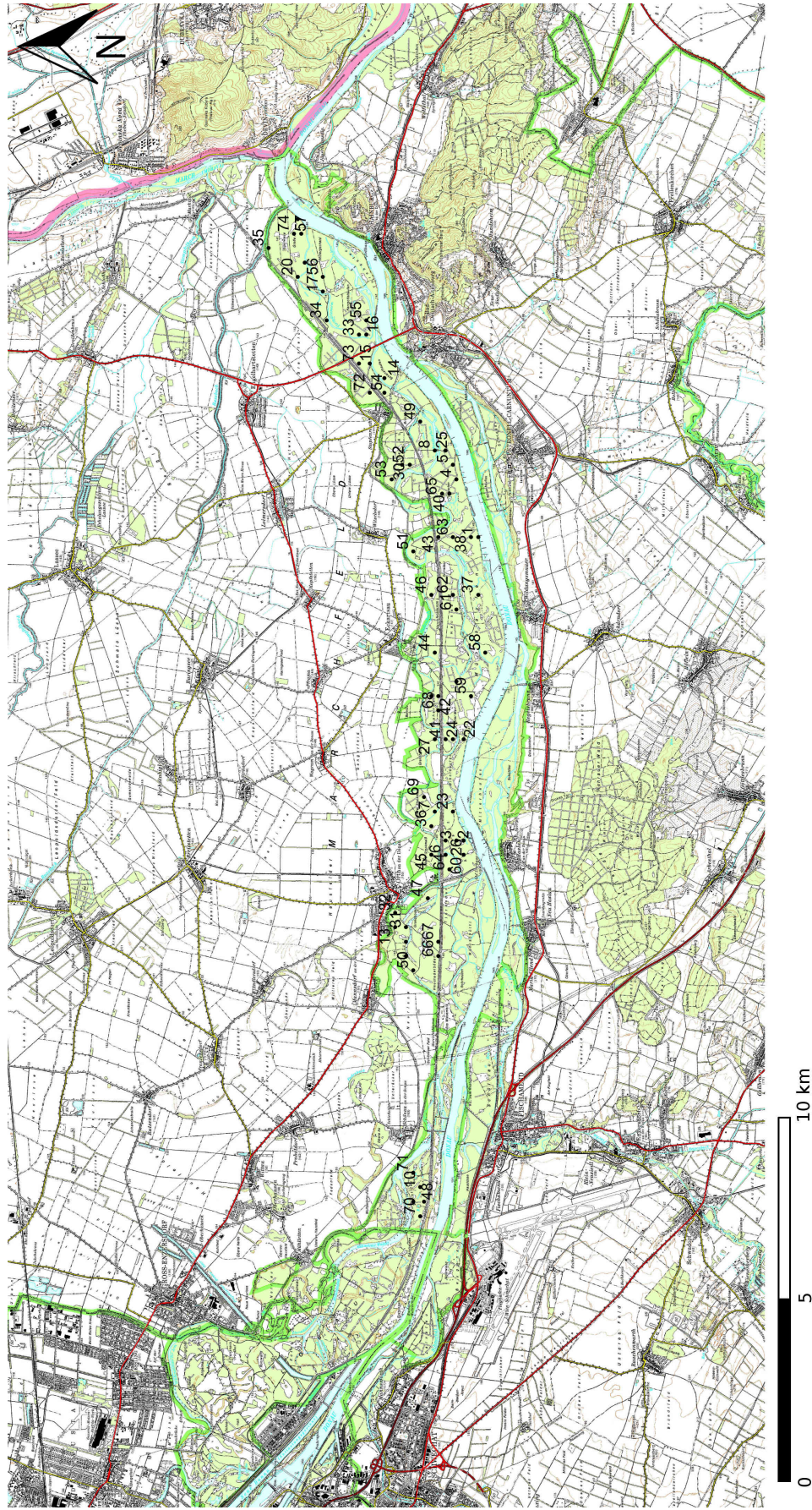


Figure 1. Map of the study area National Park Donau-Auen and the surroundings. The surveyed plots are marked and numbered.

2.3. Bird surveys

The bird assemblages were assessed by 5-minute point counts. This time span was chosen because a count duration as short as possible lowers possible effects of evasive movements, decreases the possibility of multiple counts, hence reducing pseudo-replications, and reduces the risk of declining concentration of the observer (Fuller and Langslow 1984, Rosenstock et al. 2002). Point counts are, in contrast to e.g. territory mapping relatively effort low but do have some downsides like not recording birds present but quiet (Newell et al. 2013). Nevertheless, due to limited resources point counts were favoured over territory mapping or line transects. All birds detected visually and acoustically were recorded. For each encountered individual it was noted if it was detected within or outside a 50 m radius or flying over the plot. For the subsequent analyses the individuals outside the 50 m radius and the ones flying over were not included. Some bird species, namely Common Kestrel (*Falco tinnunculus*), Common Pheasant (*Phasianus colchicus*), Eurasian Hoopoe (*Upupa epops*) and Greylag Goose (*Anser anser*) were recorded but not included in all subsequent analyses because they do not breed in the closed forests which are examined in this study. The Common Kestrel needs open land as a hunting ground, it is rather unlikely that it is breeding in a closed riparian forest (Glutz von Blotzheim 1989). The Eurasian Hoopoe is an open land bird (Glutz von Blotzheim 1994a). The Greylag Goose certainly breeds in the Donau-Auen but not in closed forests (Glutz von Blotzheim 1990). The Common Pheasant needs open space to browse and therefore to breed (Glutz von Blotzheim 1994b).

Each plot was visited three times, once during each of the following survey rounds: 08-19 April, 01-12 May and 05-16 June. The bird counts were conducted between dusk and 4 hours later because at that time the bird singing activity is high (Farina et al. 2015). Also there is no difference between those hours in bird activity (Verner and Ritter 1985), so no bias in terms of different daytime of the surveys. Also they were restricted to good weather conditions: in precipitation or storm bird calls can be missed and in cloudy and rainy conditions the bird activity may be lowered or delayed (Slagsvold 1977, Bruni et al. 2014). The order in which the plots were surveyed was changed in consecutive censuses for the following survey rounds.

2.4. Habitat variables

Distances of census points to permanent water bodies and open land were calculated with ArcMap 10.2 (ESRI). The maximum height to closed canopy (canopy height) was measured with a Nikon Laser 800 6x216.

All stems of standing dead wood with a diameter at breast height (DHB) of ≥ 10 cm were counted and their height was estimated. With these measurements the dead wood volume (deadwood) was calculated by simplifying the stems to a cylinder and extrapolate the volumes for the area.

The data of the forest inventory were provided by the Österreichische Bundesforste (ÖBf, forest holding) and the MA49 Vienna (urban administration for forestry and agriculture) and was conducted in 2013. The forest stand data consists of percentage of species per layer (lowest layer composed of thicket, second layer consists of pole crops and the highest, canopy layer comprised of tree stage wood) and forest age. The covering of the forest stands per plot was calculated using Arc.Map 10.2 (by intersecting; ESRI). With this data the forest structure variables were determined: the mean age of forest (forest age), number of woody vegetation layers (1-3), the canopy diversity (number of tree species in

highest layer, canopy diversity) and the proportion of the main tree species in the canopy layer (alder (*Alnus incana*), white poplar (*Populus alba*), ash (*Fraxinus excelsior*) and hybrid poplar (*Populus × canadensis*)). The covering of the forest stands per plot were assessed in ArcMap 10.2 (ESRI) by intersecting the plot and the forest stands and then calculate the area via field geometry.

2.5. Statistical analysis

For statistical analyses R (R Core Team 2015) and the following R packages: Betapart (Baselga 2010), Ecodist (Goslee and Urban 2007), Mass (Venables and Ripley 2002), Rcmdr (Fox 2005) and Vegan (Oksanen et al. 2016) were used as well as SPSS vers. 20 and CANOCO (Braak 1986).

The Shannon Index (also Shannon-Weaver Index, in the following SDI, Formula 1) is a diversity index (Shannon and Weaver 1998, Shannon 2001, Oksanen 2016). The calculated SDIs are based on the maximal individual number per species vs. plots matrix.

$$H = - \sum_{i=1}^S p_i \log_b p_i$$

Formula 1. Formula of Shannon Index. p_i is the proportion of species i , and S is the number of species and b is the base of the logarithm (Oksanen, 2016).

For all calculations only the bird counts within the 50m radius were considered because this is the area for which also habitat variables were available; additionally, many bird species are difficult to record out of a 50 m radius. The maximum absolute number of individuals per species over the three survey rounds (spMax) as well as the maximum SDIs over the three survey rounds (sdiMax) were used as response variables. spMax can be used as a measure for species richness, while sdiMax as a measure for species diversity, because it considers the abundance structure of the species assemblage (MacArthur and MacArthur 1961, Spellerberg and Fedor 2003). The data was not fragmented further in male, female or young and calling or singing birds. Birds flying over the plot were not considered.

To rule out spatial autocorrelation of the count data a correlogram was calculated using the x- and y-coordinate (latitude and longitude) and the Shannon Index (sdiMax). The distances follow the mean of class and never break out of the margins (Figure 2), therefore no spatial autocorrelation could be detected and hence no transformation of the data was necessary.

As significance threshold of $p \leq 0.05$ was determined for all analyses.

To examine potential relationships between predictor and response variables General Linear Models (GLMs) were calculated. Response variables for the GLMs were sdiMax and spMax (log transformed). Some predictor variables also had to be transformed because of their skewness (transformation stated in brackets). The predictor variables were the distance to water (log transformed) and open land (log transformed), the number of woody vegetation layers, the tree species diversity in the

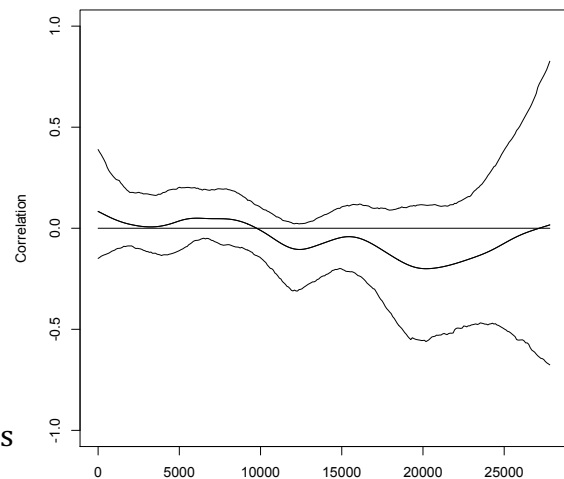


Figure 2. Correlogram with margins (based on 1000 resamples). The x-axis shows the distances and the y-axis the correlation. The correlogram is based on the geographic coordinates and the sdiMax.

canopy layer, the mean age of the forest, the dead wood volume (log transformed) and the proportions of alder, ash and alder in the canopy layer (arc sinus transformed). Not considered was the proportion of hybrid poplar because of a strong correlation with other predictors ($r > 0.4$, see Appendix 1). The other outstanding assumptions (response scaling, constant variance, residuals and outliers and influential observations) were tested and matched if necessary (Poulsen 2002). As criterion of relative model quality the Akaike Information Criterion corrected for small sample sizes ($AICc$) was used. The best model is the one with the lowest $AICc$, models with a $\Delta AICc$ value > 2 are presented in the Appendix 2 and 3 (Wagenmakers and Farrell 2004, Burnham et al. 2011, Šmilauer and Lepš 2014). The relationship diagrams are based on the GLMs with all potential variables (Appendix 4). To partition beta diversity (β_{SOE}) into effects of species turnover (β_{SIM}) and nestedness (β_{NES}), the respective measures were calculated (Baselga 2010). Bray-Curtis similarity matrices of the tree species composition (called *bcforest*) of the bird species composition (*spMax*, square root transformed to have homogenous variances, called *bcbirds*) were generated. Those Bray-Curtis matrices again were used to perform a multiple regression on distance matrices with *bcforest* as predictor to *bcbirds* (MRM, $nperm = 100$, permutations = 999). To examine a potential difference in bird assemblage in consideration of the abundances between the north- and southside of the Marchfeldschutzdamm an Analysis of Similarity (ANOSIM) with Bray-Curtis dissimilarities was calculated. As response matrix the *spMax* was used. The explanatory variable was the sides of the dam (North and South). As ordination analysis a canonical correspondence analysis (CCA) with the plot samples and species (43) was performed. The CCA infers which environmental variables explain the variation in the bird community best. This is done by computing four axes of the environmental variables in context with the species composition (Braak 1986, Jongman et al. 1995, Leyer and Wesche 2008). The ordiplot displays the 21 species, that were recorded at least in ten plots.

3. Results:

A total of 44 bird species and 3,143 individuals were counted (Table 1). The total number is divided into 2,078 individuals inside the 50 m radius, 982 individuals outside the 50 m radius and 74 individuals passing by. The total number of individuals per species for the four most abundant bird species was 569 counted individuals (403 in the 50 m radius) of Common Chaffinch (*Fringilla coelebs*), followed by Great Tit (*Parus major*) with 480 (364), Song Thrush (*Turdus philomelos*) with 293 (171) and Eurasian Blackcap (*Sylvia atricapilla*) with 197 (153) individuals. The ranking of species according to their occurrence frequency (only considering individuals recorded within the 50 m radius) proved to be identical. Common Chaffinch and Great Tit were recorded at all 72 plots, followed by Eurasian Blackcap (*Sylvia atricapilla*) and Song Thrush with records from 64 and 63 plots, respectively. Some species were recorded in much higher numbers within the 50 m radius compared to outside (e.g. Common Chaffinch, Great Tit and Eurasian Blue Tit (*Cyanistes caeruleus*)), whereas it proved to be opposite in others (e.g. Common Wood Pigeon (*Columba palumbus*), Eurasian Golden Oriole (*Oriolus oriolus*) and Common Cuckoo (*Cuculus canorus*); Table 1).

Table 1. Detected species, their total numbers of counted individuals as well as the number of individuals counted within (IN) and outside (OUT) the 50 m radius and flying over the plot; additionally, the numbers of plots with records of the respective species are provided (only considering records of individuals inside the 50 m radius). Species are ranked according to their total number of counted individuals.

English name)	Scientific name	Total individuals	IN	OUT	flying	Plots with records
Common Chaffinch	<i>Fringilla coelebs</i>	569	403	166	0	72
Great Tit	<i>Parus major</i>	480	364	114	2	72
Song Thrush	<i>Turdus philomelos</i>	293	171	122	0	63
Eurasian Blackcap	<i>Sylvia atricapilla</i>	197	153	44	0	64
Common Starling	<i>Sturnus vulgaris</i>	180	133	29	18	41
Great Spotted Woodpecker	<i>Dendrocopus major</i>	170	94	73	3	51
Eurasian Nuthatch	<i>Sitta europaea</i>	158	77	81	0	41
Common Blackbird	<i>Turdus merula</i>	147	65	81	1	40
Eurasian Blue Tit	<i>Cyanistes caeruleus</i>	135	132	3	0	60
Eurasian Wren	<i>Troglodytes troglodytes</i>	94	88	6	0	55
Common Chiffchaff	<i>Phylloscopus collybita</i>	81	60	21	0	41
European Robin	<i>Erithacus rubecula</i>	77	69	8	0	45
Collared Flycatcher	<i>Ficedula albicollis</i>	76	53	23	0	40
Eurasian Bullfinch	<i>Pyrrhula pyrrhula</i>	70	30	5	35	21
Common Wood Pigeon	<i>Columba palumbus</i>	54	6	46	2	4
Hooded/Carrion Crow	<i>Corvus corone/cornix</i>	54	8	41	5	6
Eurasian Golden Oriole	<i>Oriolus oriolus</i>	40	11	29	0	11
Common Cuckoo	<i>Cuculus canorus</i>	28	3	24	1	3
Long-tailed Tit	<i>Aegithalos caudatus</i>	27	27	0	0	12
Black Woodpecker	<i>Dryocopus martius</i>	21	2	16	3	2
European Goldfinch	<i>Carduelis carduelis</i>	16	15	1	0	15
Eurasian Jay	<i>Garrulus glandarius</i>	14	11	1	2	8
Lesser Spotted Woodpecker	<i>Dendrocopus minor</i>	13	5	8	0	5
Marsh Tit	<i>Poecile palustris</i>	13	13	0	0	9
Eurasian Treecreeper	<i>Certhia familiaris</i>	12	12	0	0	12
Eurasian Collared Dove	<i>Streptopelia decaocto</i>	11	2	9	0	1
European Green Woodpecker	<i>Picus viridis</i>	11	3	8	0	2
Wood Warbler	<i>Phylloscopus sibilatrix</i>	11	10	1	0	9
European Greenfinch	<i>Carduelis chloris</i>	10	8	2	0	5
Icterine Warbler	<i>Hippolais icterina</i>	10	8	2	0	7
Common Buzzard	<i>Buteo buteo</i>	9	2	6	1	2
European Turtle Dove	<i>Streptopelia turtur</i>	9	3	6	0	3
Common Firecrest	<i>Regulus ignicapilla</i>	8	8	0	0	7
Middle Spotted Woodpecker	<i>Dendrocopus medius</i>	7	5	2	0	4
Mistle Thrush	<i>Turdus viscivorus</i>	5	4	0	1	4
Spotted Flycatcher	<i>Muscicapa striata</i>	5	5	0	0	4
Willow Warbler	<i>Phylloscopus trochilus</i>	5	5	0	0	5
Short-toed Treecreeper	<i>Certhia brachydactyla</i>	4	4	0	0	4
Yellowhammer	<i>Emberiza citrinella</i>	3	2	1	0	2
Stock Dove	<i>Columba oenas</i>	3	0	3	0	3
European Serin	<i>Serinus serinus</i>	1	1	0	0	1
Goldcrest	<i>Regulus regulus</i>	1	1	0	0	1
Lesser Whitethroat	<i>Sylvia curruca</i>	1	1	0	0	1
White Wagtail	<i>Motacilla alba</i>	1	1	0	0	1
Total	44	3134	2078	982	74	859

3.1. Species richness and diversity

The best model evaluating effects of forest structure and landscape variables on spMax (Table 2) includes four predictors: distance to water, canopy diversity and proportions of white poplar and alder in the canopy layer. In this model (and all subsequent models with a $\Delta AICc \leq 2$) the distance to water and the proportion of alder have a significant effect. There are no other significant predictor variables in any model. The distance to water has a negative effect and the proportion of alder has a positive effect (Table 2, Figure 3 and 4). For details of the model selection see Appendix 2 and 3 (all GLMs with a $\Delta AICc \leq 5$).

Table 2. Best GLMs (based on Akaike model selection; compare Appendix 2) assessing effects of seven different variables quantifying forest structure (forest age, canopy diversity, canopy height proportion of white poplar, proportion of alder, proportion of ash and deadwood volume and two landscape variables (distance to water bodies and openland) on spMax. Model estimates, standard errors, *t*- and *p*-values are shown for all variables included in the 14 best GLMs (with $\Delta AICc \leq 2$). A significant *p*-value (≤ 0.05) is additionally marked with an *.

Model / Independent variables	Est.	SE	<i>t</i>	<i>p</i>	
Best					
(Intercept)	2.91	0.18	16.10	<0.0001	*
distance to water	-0.07	0.03	-2.07	0.0420	*
canopy diversity	-0.03	0.01	-1.80	0.0771	
white poplar	-0.09	0.05	-1.61	0.1115	
alder	0.83	0.42	2.00	0.0494	*
2nd					
(Intercept)	2.91	0.18	15.90	<0.0001	*
distance to water	-0.08	0.03	-2.31	0.0240	*
canopy diversity	-0.02	0.01	-1.61	0.1129	
alder	0.86	0.42	2.04	0.0452	*
3rd					
(Intercept)	2.65	0.20	13.48	<0.0001	*
distance to water	-0.06	0.03	-1.84	0.0701	
forest age	0.00	0.00	1.56	0.1225	
alder	0.77	0.42	1.86	0.0678	
4th					
(Intercept)	2.80	0.17	16.19	<0.0001	*
distance to water	-0.07	0.03	-2.12	0.0381	*
alder	0.74	0.42	1.77	0.0808	
5th					
(Intercept)	2.80	0.17	16.24	<0.0001	*
distance to water	-0.06	0.03	-1.88	0.0645	
alder	0.71	0.42	1.70	0.0936	
white poplar	-0.08	0.06	-1.40	0.1668	
6th					
(Intercept)	2.77	0.22	12.79	<0.0001	*
distance to water	-0.07	0.03	-2.02	0.0469	*
canopy diversity	-0.02	0.01	-1.25	0.2151	
forest age	0.00	0.00	1.20	0.2350	
alder	0.86	0.42	2.05	0.0448	*
7th					
(Intercept)	2.66	0.20	13.56	<0.0001	*
distance to water	-0.06	0.03	-1.67	0.0992	
forest age	0.00	0.00	1.37	0.1766	
white poplar	-0.07	0.06	-1.18	0.2436	
alder	0.74	0.42	1.78	0.0795	
8th					
(Intercept)	2.94	0.19	15.73	<0.0001	*
distance to water	-0.07	0.03	-2.12	0.0382	*
canopy diversity	-0.03	0.01	-1.88	0.0640	
ash	-0.05	0.07	-0.70	0.4883	
white poplar	-0.10	0.06	-1.75	0.0853	
alder	0.89	0.43	2.09	0.0406	*

9th					
(Intercept)	2.94	0.19	15.73	<0.0001	*
distance to water	-0.07	0.03	-2.12	0.0382	*
canopy diversity	-0.03	0.01	-1.88	0.0640	
ash	-0.05	0.07	-0.70	0.4883	
white poplar	-0.10	0.06	-1.75	0.0853	
alder	0.89	0.43	2.09	0.0406	*
10th					
(Intercept)	2.96	0.18	16.25	<0.0001	*
distance to water	-0.08	0.03	-2.37	0.0205	*
canopy diversity	-0.02	0.01	-1.45	0.1509	
white poplar	-0.09	0.06	-1.65	0.1027	
11th					
(Intercept)	2.88	0.17	16.81	<0.0001	*
distance to water	-0.08	0.03	-2.46	0.0163	*
12th					
(Intercept)	2.86	0.17	16.86	<0.0001	*
distance to water	-0.08	0.03	-2.19	0.0319	*
white poplar	-0.08	0.06	-1.48	0.1439	
13th					
(Intercept)	2.73	0.20	14.00	<0.0001	*
distance to water	-0.08	0.03	-2.21	0.0306	*
forest age	0.00	0.00	1.46	0.1489	
14th					
(Intercept)	2.80	0.17	16.19	<0.0001	*
distance to water	-0.07	0.03	-2.12	0.0381	*
alder	0.74	0.42	1.77	0.0808	

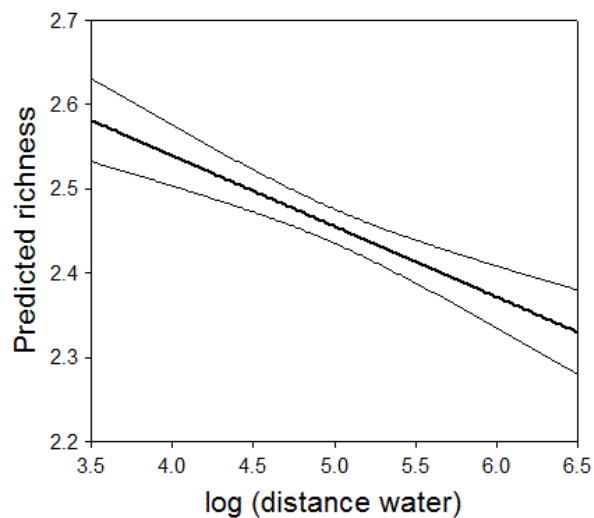


Figure 3. Relationship between species richness (log-transformed) predicted by GLM including all forest structure and landscape variables and distance of census points to the nearest water bodies.

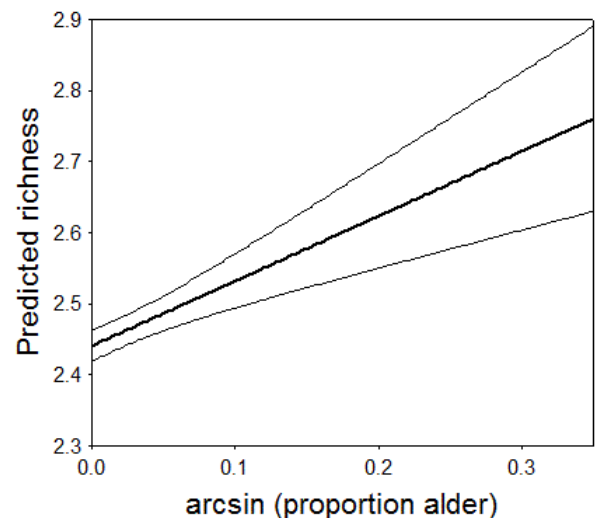


Figure 4. Relationship between species richness (log-transformed) predicted by GLM including all forest structure and landscape variables and proportion of alder in the canopy layer.

The best model for sdiMax (Table 3) includes three predictors: proportion of white poplar and alder and the dead wood volume. All these three predictors have a significant effect on the sdiMax in this model (and in all subsequent models with a $\Delta AIC \leq 2$) (Table 3). There are no other significant predictor variables in any model. The proportion of white poplar in the canopy layer has a negative effect on the sdiMax (Table 3, Figure 5) while the proportion of alder has a positive effect (Table 3, Figure 6). The deadwood volume has a negative effect on the sdiMax (Table 3, Figure 7).

Table 3. Best GLMs (based on Akaike model selection, compare Appendix 3) assessing effects of seven different variables quantifying forest structure (forest age, canopy diversity, canopy height, proportion of white poplar, proportion of alder, proportion of ash and deadwood volume and two landscape variables (distance to water bodies and openland) on sdiMax. Model estimates, standard errors, *t*- and *p*-values are shown for all variables included in the four best GLMs (with $\Delta AICc \leq 2$). A significant *p*-value (≤ 0.05) is additionally marked with an *.

Model / Independent variable	Est.	SE	<i>t</i>	<i>p</i>	
Best					
(Intercept)	2.95	0.14	20.47	<0.0001	*
white poplar	-0.10	0.05	-2.18	0.0324	*
alder	0.79	0.34	2.33	0.0230	*
Deadwood	-0.02	0.01	-2.14	0.0360	*
2nd					
(Intercept)	2.91	0.15	19.35	<0.0001	*
forest age	0.00	0.00	0.95	0.3472	
white poplar	-0.09	0.05	-1.97	0.0532	
alder	0.80	0.34	2.35	0.0218	*
Deadwood	-0.02	0.01	-2.24	0.0286	*
3rd					
(Intercept)	3.08	0.21	14.99	<0.0001	*
distance to water	-0.02	0.03	-0.87	0.3861	
white poplar	-0.09	0.05	-2.01	0.0484	*
alder	0.74	0.35	2.13	0.0370	*
deadwood	-0.02	0.01	-2.17	0.0339	*
4th					
(Intercept)	2.97	0.15	19.99	<0.0001	*
white poplar	-0.11	0.05	-2.23	0.0292	*
ash	-0.03	0.06	-0.54	0.5937	
alder	0.83	0.35	2.37	0.0206	*
deadwood	-0.02	0.01	-2.17	0.0338	*

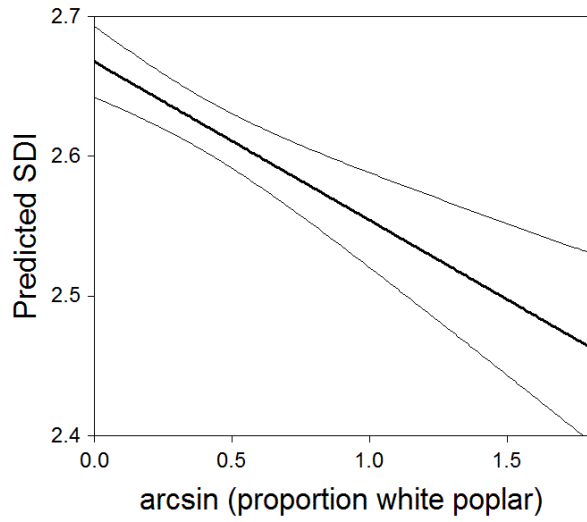


Figure 5. Relationship between Shannon diversity index predicted by GLM including all forest structure and landscape variables and proportion of white poplar in the canopy layer.

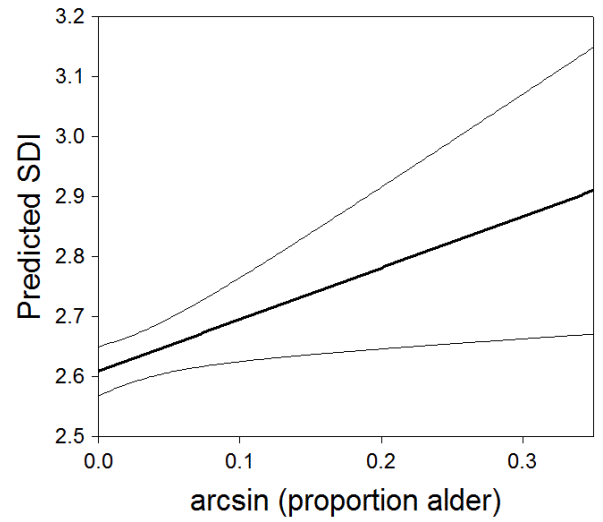


Figure 6. Relationship between Shannon diversity index predicted by GLM including all forest structure and landscape variables and proportion of alder in the canopy layer.

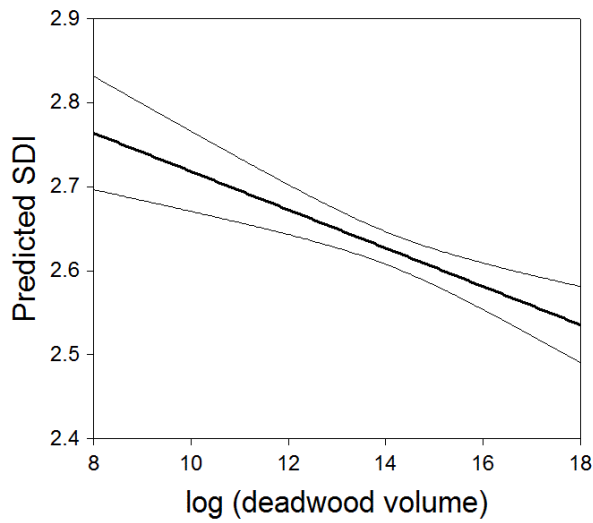


Figure 7. Relationship between Shannon diversity index predicted by GLM including all forest structure and landscape variables and deadwood volume.

3.2. Species composition

The overall beta diversity for bird assemblages recorded at 72 census points achieved a β_{SOR} value of 0.93. Nestedness contributed only weakly ($\beta_{\text{NES}} = 0.03$) to overall beta diversity. In contrary, species turnover was responsible for most of the recorded beta diversity ($\beta_{\text{SIM}} = 0.90$).

There is no significant relationship between the predictor tree species composition and the response bird species composition (forest and bird matrices) in the MRMmax (Table 4).

Table 4. MRMmax with its R^2 , R^2 - p , F - and F - p - values as well as the p -values of the intercept and Bray-Curtis matrices.

	bcdist (birds)	p	R^2	R^2 - p	F	F - p
MRMmax			<0.01	0.43	4.94	0.43
Int	0.35	0.81				
bcdist(forest)	0.01	0.43				

Further, species composition did not differ significantly between areas north and south of the Marchfeldschutzdamm (one-way ANOSIM: Global $R = 0.05$, $p = 0.06$).

3.3. Habitat preferences of species

A CCA was generated of the species composition and site data. The *Eigenvalues* of the CCA-axes were: (1): 0.069, (2): 0.052, (3): 0.045 and (4): 0.031. The total inertia (sum of Eigenvalues, value of total variance in species dispersion) is 2.087. The amount of total variation that is explained by the environmental variables is 29 % (0.294). The variance cumulative variance of the axes is (1): 3.3 %, (2): 5.9 %, (3): 8% and (4): 9.5 % carrying a Pearson's species environment correlation of (1): 0.813, (2): 0.678, (3): 0.727 and (4): 0.583 respectively. The ordination graphics show the environmental variables represented by arrows and are constructed in link with the site data (Figure 8) and species (Figure 9). Neither in the site graphic nor in the species graphic any clear clusters could be distinguished. In contrast, most species are aggregating in the centre of the ordination indicating a high tolerance against most assessed habitat variables.

Interpreting the length of the arrows (Figure 8 and 9) deadwood distance to open land and canopy diversity have the highest impact on axis 1, while canopy height and distance to water have the highest influence on axis 2. The impact of alder, white poplar and forest age seem relatively low. But we know that the third and fourth axis still account for 8% and 9.5% of the cumulative variance so those variables with shorter arrow can have high impacts on those axes.

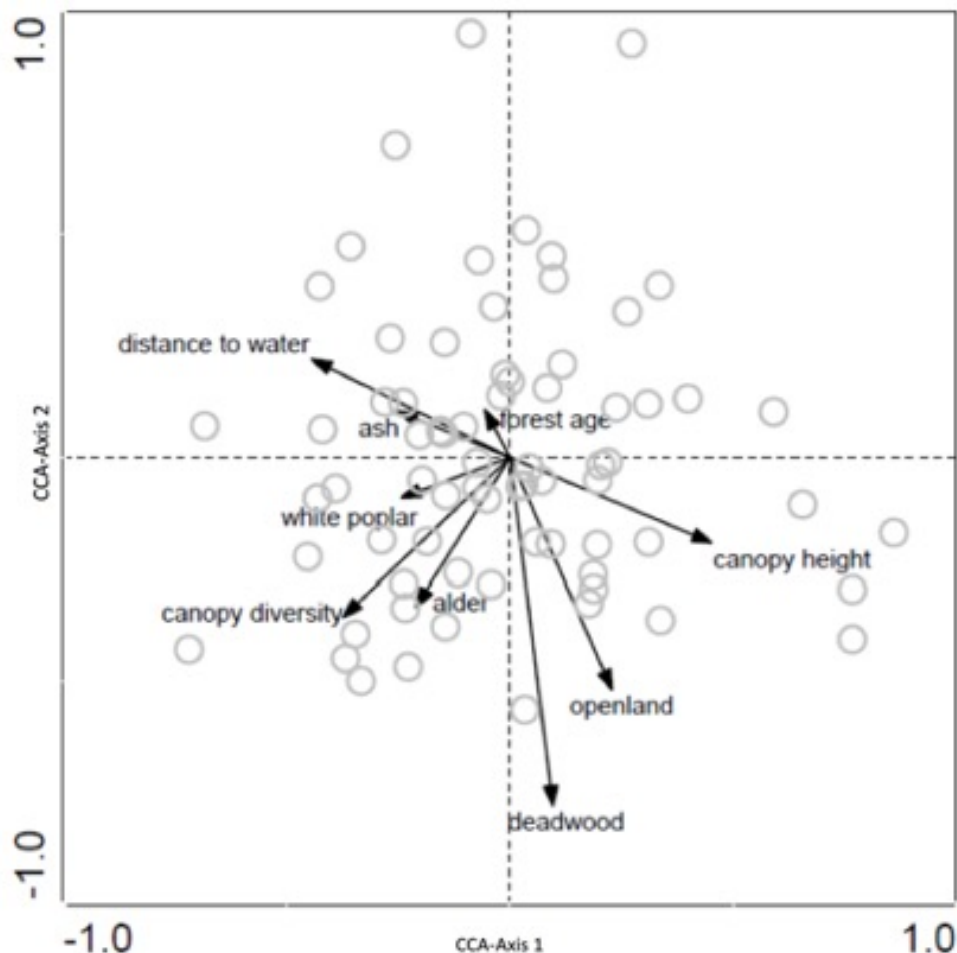


Figure 8. Ordination plot of site data defined by the axes of the CCA. Length and angle of the arrows indicate the direction and strength of correlation explained by the environment variables to the ordination axes (Jongmann et al 1995).

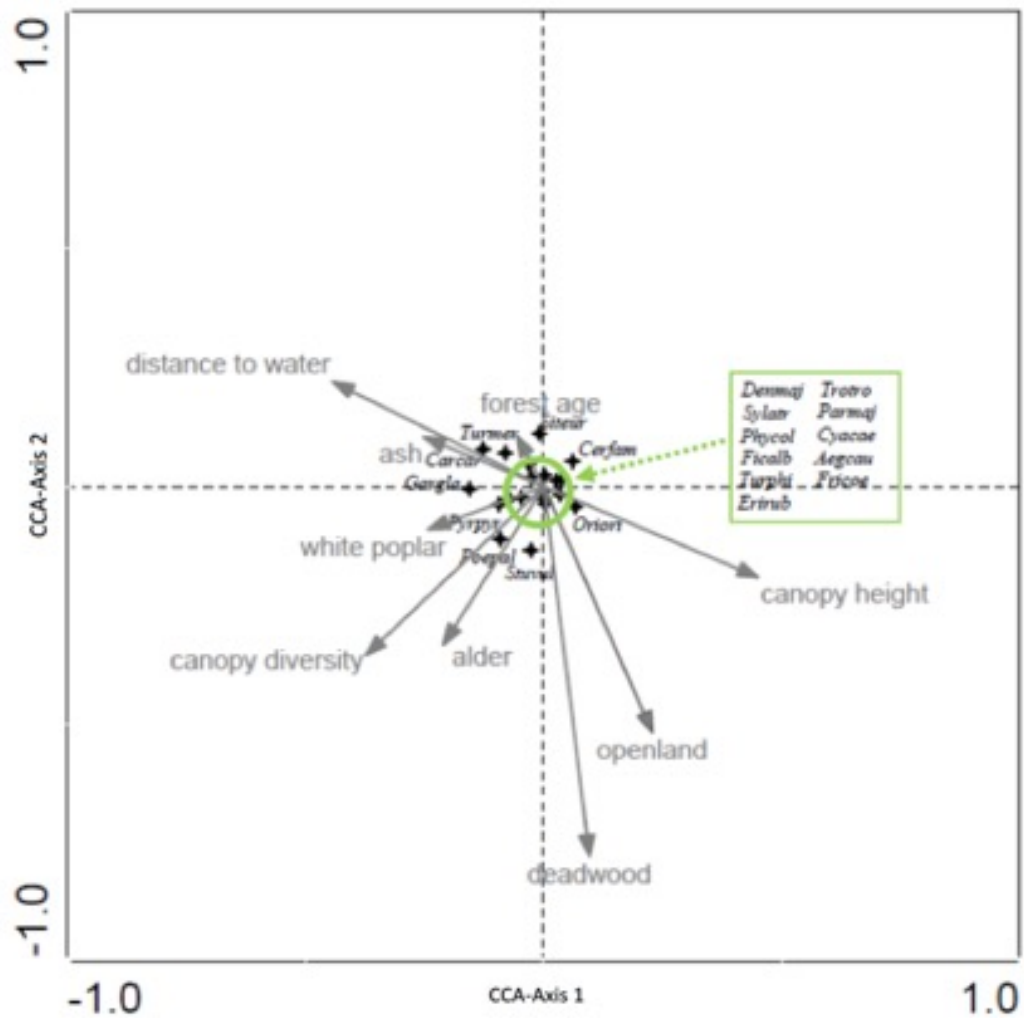


Figure 9. Ordination plot of species defined by the axes of the CCA showing the twenty most common bird species (inside the 50 m radius) on ordination plane in connection to the environment variables. Species name-shortcuts are conducted through the first three letters of the first and second scientific name of the species.

4. Discussion:

4.1. Forest structure and landscape: effects on species richness and diversity

In accordance with our hypotheses, we found effects of forest structure and landscape elements on floodplain forest bird species richness and diversity. Species richness of forest birds increased with decreasing distance to water bodies and increasing proportion of alder trees in the canopy layer. Similarly, bird species diversity was highest at forest sites with high proportions of alder. In contrast, species diversity was negatively affected by an increasing proportion of white poplar and, surprisingly, by an increasing volume of dead wood.

The differences between the models of the two values for species richness and species diversity can be explained by the differences in their formation. The species richness is built by the simple maximum species number, while the Shannon Diversity Index also takes the abundances into account and is therefore a more complex value. Nonetheless they are related and their significant predictors will not be discussed separately.

According to Gabbe et al. (2002), “the tree species composition of forests can be an important component of habitat selection of breeding birds (...)”, which was also found in several other studies in various forest ecosystems (Willson 1974, Rov 1975, Holmes and Robinson 1981, James and Wamer 1982, Rotenberry 1985, Hewson et al. 2011, Fuller and Rothery 2013, Birčák and Reif 2015, Munes et al. 2015). The results of this study suggest an influence of tree species on the bird species richness and diversity; reflected through the effect of the proportion of alder and white poplar in the canopy. The white poplar grows in the riparian forest rather at more drier parts while the alder is an indicator for stagnant moisture and high groundwater (Ellenberg et al. 2010). This could indicate that bird richness and diversity become higher at more humid sites. This is compliant to the result that the distance to permanent water bodies has a negative effect to the bird richness. This was an expected finding because there is a positive relation between distance to water and the emergence of adult aquatic insects which represent an important food source for many breeding birds (Iwata et al. 2003, Sullivan et al. 2007). This result would also indicate that the effect can't be counterbalanced by terrestrial insects feeding on riparian plants (Sullivan et al. 2007). A possible explanation is the sheer amount of adult aquatic insect consumed. Nakano and Murakami (2001) estimated that adult aquatic insects make more than a quarter of the annual total energy budget of the riparian bird community. Additionally, before the foliage season prey availability might be limited to aquatic insects. But this time is also the crucial pre-breeding period where female birds must accumulate reserves for egg-production (Tye 1992, Matsuoka et al. 1997). Due to the lack of terrestrial prey biomass during spring they rely exceedingly on adult aquatic insects emerging from streams (Iwata et al. 2003). Moreover, the nestlings of some bird species might depend on insect nourishment (Thomas 2001).

Several studies report a positive relationship between bird richness and diversity and dead wood volume (Nilsson 1979, Birčák and Reif 2015, Mag and Ódor 2015). Standing dead wood provides overwintering and feeding locations for insects and indicates a dense foliage likely promoting an insect community with high densities (Nilsson 1979) which supports insectivorous birds. Also dead wood is a very important source for primary (e.g.

woodpeckers) and secondary cavity nesters (e.g. tits, nuthatches and treecreepers) (Redolfi De Zan et al. 2016). Species diversity decreases with the amount of dead wood in this study. This might be due to the fact that a lot of sites with standing dead wood were economically used until recently. When the National Park was established any forest use measures were stopped, including thinning of recently planted trees. This resulted in a lot of young and small trees dying off. These small stems account to the volume of dead wood but aren't attractive for birds. Rather, a high density of such thin dead trees may indicate formerly heavily exploited forest stands with a low structural diversity. Consequently, such forest sites may be characterized by decreased bird diversity. The typically positive relationship between forest age and bird richness and diversity, respectively (James and Wamer 1982, Sullivan et al. 2007, Hewson et al. 2011, Fuller and Rothery 2013, Birčák and Reif 2015) could not be confirmed in this study. This might be due to the intensive forestry management until 20 years ago. Accordingly, the youngest forests are 20 years old while the oldest are 98 years old. The mean forest age is 49.1 (± 18.88) years. On the one hand there are still a lot of relicts of the forestry 20 years ago, but on the other hand there are not so many recently used and therefore succession stands. Floods are not that severe that they affect forest age. In other words, the forest age might not build a gradient upon which bird diversity takes shape. Also the distance to open land did not affect neither bird species richness nor diversity. In fact, all selected census points had to be located in a distance of at least 50 m to the nearest forest margin. The depth of most recognized edge effects is greater than or at least close to 50 m (Laurance et al. 2002, Ewers and Banks-Leite 2013, Neate-Clegg et al. 2016). Hence, edge effects may not have been prominent enough to affect bird assemblages. Further, many open land sites, such as small meadows embedded in the matrix of the floodplain forest, may have been too small to provide an adequate habitat for "edge species". Canopy diversity was included in several of the best models evaluating effects of forest structure and landscape variables on bird richness but did not achieve a significant level. In contrast, canopy height did not prove to affect bird species richness and diversity at all. Canopy height could be a surrogate for an increased complexity of available micro-habitat elements, potentially increasing the availability of various resources for birds. However, particularly the micro structure of the understory, an important predictor of habitat quality for many forest species, is difficult to quantify reliably (Fuller and Rothery 2013).

4.2. Species composition and habitat preferences

Changes in species composition were predominantly driven by species turnover, which accounted for 90% of the beta diversity. Remarkably, we could not detect any relationships between measured habitat and landscape variables and bird species composition, indicating that stochastic phenomena may shape bird assemblages within the small-grained mosaic of forest types differing in factors such as plant composition, vegetation structure and food availability.

Though expected, the species composition did not differ between forest stands located north and south of the flood protection dam. A possible explanation is that areas, also ones that are not protected by the dam, lack regular flooding because the Danube is regulated and therefore flooding is less frequent (Margl 1973, Schratt-Ehrendorfer 2011). Additionally, the Danube has deepened its bed (ViaDonau 2016b) resulting in decreasing hydrological connectivity between the river and the adjacent floodplains. Those parts which are flooded rarely get raised groundwater at high water events. But this is also the

case for the areas south of the dam (Brix 1972). Today, the riparian forests north and south of the dam might be affected mainly from rising ground water, while additional flooding events affecting forest areas between the Danube and the flood protection dam may be too rare to shape bird assemblages.

Evaluating relationships between individual bird species in floodplain forests and environmental parameters used in this study did not indicate any strong responses. This is either emphasizing that the species are relatively resistant against changes in the measured habitat and landscape variables or that the mosaic of differentially structured forest patches is too small-grained to maintain distinct species assemblages. It remains to be studied in detail if the pronounced spatial heterogeneity of forest types generated by flooding events, human impact due river regulation or former forestry measures is responsible for this situation.

4.3. Conservation implications

The existence of a relationship between bird diversity and environment variables suggests that habitat heterogeneity, specifically structure and floristic elements, should be key to conservation plans and measures (Hewson et al. 2011). For the National Park Donau-Auen this particularly means maintaining a high lateral hydrological connectivity between the river Danube and its floodplains, including the restoration of side arms. Human suppression of disturbance regimes has been emphasized as a main driver of the decline of bird species in floodplain systems (Munes et al. 2015). This study also provides some evidence that there is no clear segregation of bird assemblages along the investigated softwood-hardwood forest gradient anymore. Rather, bird assemblages of the floodplain forests are currently shaped by food availability and perhaps differences of forest stands caused by varying accessibility to rising groundwater.

5. References

- Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity: Partitioning beta diversity. - *Global Ecology and Biogeography* 19: 134–143.
- Batáry, P., Fronczek, S., Normann, C., Scherber, C. and Tschardtke, T. 2014. How do edge effect and tree species diversity change bird diversity and avian nest survival in Germany's largest deciduous forest? - *Forest Ecology and Management* 319: 44–50.
- Birčák, T. and Reif, J. 2015. The effects of tree age and tree species composition on bird species richness in a Central European montane forest. - *Biologia* 70: 1528–1536.
- Bobiec, A. 2002. Living stands and dead wood in the Białowieża forest: suggestions for restoration management. - *Forest Ecology and Management* 165: 125–140.
- Braak, C. J. F. T. 1986. Canonical Correspondence Analysis: A New Eigenvector Technique for Multivariate Direct Gradient Analysis. - *Ecology* 67: 1167–1179.
- Brix, F. 1972. Die Aulandschaft: Hydrologie, Geologie und Bodenkunde. - In: *Naturgeschichte Wiens*. Böhlau, pp. 499–530.
- Bruni, A., Mennill, D. J. and Foote, J. R. 2014. Dawn chorus start time variation in a temperate bird community: relationships with seasonality, weather, and ambient light. - *Journal of Ornithology* 155: 877–890.
- Buffington, J. M., Kilgo, J. C., Sargent, R. A. and Miller, K. V. 1997. Comparison of Breeding Bird Communities in Bottomland Hardwood Forests of Different Successional Stages. - *The Wilson Bulletin* 109: 314–319.
- Bundeskanzleramt 1983. BGBl Nr. 225/1983. ris.bka.gv.at.
- Bundeskanzleramt 1996. BGBl Nr. 653/1996. ris.bka.gv.at.
- Burnham, K. P., Anderson, D. R. and Huyvaert, K. P. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. - *Behavioral Ecology and Sociobiology* 65: 23–35.
- Christen, W. 1983. Brutvogelbestände in Wäldern unterschiedlicher Baumarten- und Altersklassenzusammensetzung. - *Der Ornithologische Beobachter*: 281–291.
- Ellenberg, H., Leuschner, C. and Dierschke, H. 2010. Vegetation Mitteleuropas mit den Alpen: in ökologischer, dynamischer und historischer Sicht. - Ulmer.
- Ewers, R. M. and Banks-Leite, C. 2013. Fragmentation Impairs the Microclimate Buffering Effect of Tropical Forests (G Bohrer, Ed.). - *PLoS ONE* 8: e58093.
- Farina, A., Ceraulo, M., Bobryk, C., Pieretti, N., Quinci, E. and Lattanzi, E. 2015. Spatial and temporal variation of bird dawn chorus and successive acoustic morning activity in a Mediterranean landscape. - *Bioacoustics* 24: 269–288.

- Fehér, J., Gáspár, J., Szurdiné Veres, K., Kiss, A., Austnes, K., Globevnik, L., Kirn, T., Peterlin, M., Stein, U., Spiteri, C., Prins, T., Deltares, S., Laukkonen, E., Heiskanen, A.-S., Semerádová, S., Künitzer, A. and Kristensen, P. 2012. Hydromorphological alterations and pressures in European rivers, lakes, transitional and coastal waters: thematic assessment for EEA Water 2012 Report. - European Topic Centre on Inland, Coastal and Marine Waters.
- Felton, A., Hedwall, P. O., Lindbladh, M., Nyberg, T., Felton, A. M., Holmström, E., Wallin, I., Löf, M. and Brunet, J. 2016. The biodiversity contribution of wood plantations: Contrasting the bird communities of Sweden's protected and production oak forests. - *Forest Ecology and Management* 365: 51–60.
- Figarski, T. and Kajtoch, Ł. 2015. Alterations of riverine ecosystems adversely affect bird assemblages. - *Hydrobiologia* 744: 287–296.
- Fox, J. 2005. Rcmdr.
- Fox, J. W. 2013. The intermediate disturbance hypothesis should be abandoned. - *Trends in Ecology & Evolution* 28: 86–92.
- Fuller, R. J. and Langslow, D. R. 1984. Estimating numbers of birds by point counts: how long should counts last? - *Bird study* 31: 195–202.
- Fuller, R. J. and Rothery, P. 2013. Temporal consistency in fine-scale habitat relationships of woodland birds during a period of habitat deterioration. - *Forest Ecology and Management* 289: 164–174.
- Gabbe, A. P., Robinson, S. K. and Brawn, J. D. 2002. Tree-Species Preferences of Foraging Insectivorous Birds: Implications for Floodplain Forest Restoration. - *Conservation Biology* 16: 462–470.
- Glutz von Blotzheim, U. 1989. *Handbuch der Vögel Mitteleuropas* 4: Falconiformes. - Aula.
- Glutz von Blotzheim, U. 1990. *Handbuch der Vögel Mitteleuropas* 2: Anseriformes (1). - Aula.
- Glutz von Blotzheim, U. 1994a. *Handbuch der Vögel Mitteleuropas* 9: Columbiformes - Piciformes. - Aula.
- Glutz von Blotzheim, U. 1994b. *Handbuch der Vögel Mitteleuropas* 5: Galliformes und Gruiformes. - Aula.
- Goslee, S. C. and Urban, D. L. 2007. Ecodist.
- Hagan, J. M., McKinley, P. S., Meehan, A. L. and Grove, S. L. 1997. Diversity and Abundance of Landbirds in a Northeastern Industrial Forest. - *The Journal of Wildlife Management* 61: 718.
- Helle, P. and Järvinen, O. 1986. Population Trends of North Finnish Land Birds in Relation to Their Habitat Selection and Changes in Forest Structure. - *Oikos* 46: 107.

- Hewson, C. M., Austin, G. E., Gough, S. J. and Fuller, R. J. 2011. Species-specific responses of woodland birds to stand-level habitat characteristics: The dual importance of forest structure and floristics. - *Forest Ecology and Management* 261: 1224–1240.
- Holmes, R. T. and Robinson, S. K. 1981. Tree Species Preferences of Foraging Insectivorous Birds in a Northern Hardwoods Forest. - *Oecologia* 48: 31–35.
- IUCN 2007. Species extinction. iucn.org.
- IUCN 2015. Wher the blue Danube goes green. iucn.org.
- Iwata, T., Nakano, S. and Murakami, M. 2003. Stream meanders increase insectivorous bird abundance in riparian deciduous forests. - *Ecography* 26: 325–337.
- James, F. C. and Wamer, N. O. 1982. Relationships between Temperate Forest Bird Communities and Vegetation Structure. - *Ecology* 63: 159–171.
1995. Data analysis in community and landscape ecology (RH Jongman, CJF ter Braak, and OFR Van Tongeren, Eds.). - Cambridge University Press.
- Laurance, W. F., Lovejoy, T. E., Vasconcelos, H. L., Bruna, E. M., Didham, R. K., Stouffer, P. C., Gascon, C., Bierregaard, R. O., Laurance, S. G. and Sampaio, E. 2002. Ecosystem Decay of Amazonian Forest Fragments: a 22-Year Investigation. - *Conservation Biology* 16: 605–618.
- Leyer, I. and Wesche, K. 2008. Multivariate Statistik in der Ökologie: eine Einführung. - Springer.
- MacArthur, R. H. and MacArthur, J. W. 1961. On Bird Species Diversity. - *Ecology* 42: 594–598.
- Mag, Z. and Ódor, P. 2015. The effect of stand-level habitat characteristics on breeding bird assemblages in Hungarian temperate mixed forests. - *Community Ecology* 16: 156–166.
- Margl, H. 1973. Pflanzengesellschaften und ihre standortgebundene Verbreitung in teilweise abgedämmten Donauauen (Untere Lobau). - In: Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien. pp. 5–51.
- Matsuoka, S. M., Handel, C. M., Roby, D. D. and Thomas, D. L. 1997. The Relative Importance of Nesting and Foraging Sites in Selection of Breeding Territories by Townsend's Warblers. - *The Auk* 114: 657–667.
- McCallum, M. L. 2015. Vertebrate biodiversity losses point to a sixth mass extinction. - *Biodiversity and Conservation* 24: 2497–2519.
- Mosimann, P., Naef-Daenzer, B. and Blattner, M. 1987. Die Zusammensetzung der Avifauna in typischen Waldgesellschaften der Schweiz. - *Der Ornithologische Beobachter*: 275–299.

- Munes, E. C., Dixon, M. D., Swanson, D. L., Merkord, C. L. and Benson, A. R. 2015. Large, infrequent disturbance on a regulated river: response of floodplain forest birds to the 2011 Missouri River flood. - *Ecosphere* 6: 1–19.
- Nakano, S. and Murakami, M. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. - *Proceedings of the National Academy of Sciences* 98: 166–170.
- National Park Donau-Auen 2016. donauauen.at.
- Neate-Clegg, M. H. C., Morshuis, E. C. and Banks-Leite, C. 2016. Edge effects in the avifaunal community of riparian rain-forest tracts in Tropical North Queensland. - *Journal of Tropical Ecology* 32: 280–289.
- Newell, F. L., Sheehan, J., Wood, P. B., Rodewald, A. D., Buehler, D. A., Keyser, P. D., Larkin, J. L., Beachy, T. A., Bakermans, M. H., Boves, T. J., Evans, A., George, G. A., McDermott, M. E., Perkins, K. A., White, M. B. and Wigley, T. B. 2013. Comparison of point counts and territory mapping for detecting effects of forest management on songbirds. - *Journal of Field Ornithology* 84: 270–286.
- Nilsson, S. G. 1979. Density and Species Richness of Some Forest Bird Communities in South Sweden. - *Oikos* 33: 392.
- Oksanen, J. 2016. Vegan ecological diversity. cran.r-project.org.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. and Wagner, H. 2016. *Vegan*.
- Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M. and Sexton, J. O. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. - *Science* 344: 1246752.
- Poulsen, B. O. 2002. Avian richness and abundance in temperate Danish forests: tree variables important to birds and their conservation. - *Biodiversity & Conservation* 11: 1551–1566.
- R Core Team 2015. *R*. R-foundation for statistical computing.
- Redolfi De Zan, L., de Gasperis, S. R., Fiore, L., Battisti, C. and Carpaneto, G. M. 2016. The importance of dead wood for hole-nesting birds: a two years study in three beech forests of central Italy. - *Israel Journal of Ecology & Evolution*: 1–9.
- Rosenstock, S. S., Anderson, D. R., Giesen, K. M., Leukering, T. and Carter, M. F. 2002. Landbird counting techniques: current practices and an alternative. - *The Auk* 119: 46–53.
- Rotenberry, J. T. 1985. The Role of Habitat in Avian Community Composition: Physiognomy or Floristics? - *Oecologia* 67: 213–217.

- Rov, N. 1975. Breeding Bird Community Structure and Species Diversity along an Ecological Gradient in Deciduous Forest in Western Norway. - *Ornis Scandinavica* 6: 1.
- Saab, V. 1999. Importance of Spatial Scale to Habitat Use by Breeding Birds in Riparian Forests: A Hierarchical Analysis. - *Ecological Applications* 9: 135.
- Schratt-Ehrendorfer, L. 2011. Doanu und Auenlandschaft Ein Lebensraum voller Gegensätze. - In: Berger, R. and Ehrendorfer, F. (eds), *Ökosystem Wien: die Naturgeschichte einer Stadt. Reihe "Wiener Umweltstudien."* Böhlau, pp. 328–390.
- Shannon, C. E. 2001. A mathematical theory of communication. - *Acm Sigmoble Mobile Computing and Communications Review* 5: 3.
- Shannon, C. E. and Weaver, W. 1998. The mathematical theory of communication. - Univ. of Illinois Press.
- Slagsvold, T. 1977. Bird Song Activity in Relation to Breeding Cycle, Spring Weather, and Environmental Phenology. - *Ornis Scandinavica* 8: 197.
- Šmilauer, P. and Lepš, J. 2014. Multivariate analysis of ecological data using Canoco 5. - Univ. Press.
- Sommerwerk, N., Hein, T., Schneider-Jakoby, M., Baumgartner, C., Ostojić, A., Paunović, M., Bloesch, J., Siber, R. and Tockner, K. 2009. The Danube river basin. - *Rivers of Europe*: 59–112.
- Spellerberg, I. F. and Fedor, P. J. 2003. A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the "Shannon-Wiener" Index: On species richness and diversity. - *Global Ecology and Biogeography* 12: 177–179.
- Sullivan, S. M. P., Watzin, M. C. and Keeton, W. S. 2007. A riverscape perspective on habitat associations among riverine bird assemblages in the Lake Champlain Basin, USA. - *Landscape Ecology* 22: 1169–1186.
- Tepper, G. H. 2010. Species diversity and extinction. - Nova Science Publishers.
- Teufelbauer, N. and Frank, G. 2009. Donauauen östlich von Wien. - In: Dvořák, M. et al. (eds), *Important bird areas: die wichtigsten Gebiete für den Vogelschutz in Österreich.* Naturhistorisches Museum, pp. 130–147.
- Thomas, D. W. 2001. Energetic and Fitness Costs of Mismatching Resource Supply and Demand in Seasonally Breeding Birds. - *Science* 291: 2598–2600.
- Tockner, K. and Stanford, J. A. 2002. Riverine flood plains: present state and future trends. - *Environmental conservation* 29: 308–330.
- Tomialojc, L. and Wesolowski, T. 1994. Die Stabilität der Vogelgemeinschaft in einem Urwald der gemässigten Zone: Ergebnisse einer 15jährigen Studie aus dem

- Nationalpark von Bialowieza (Polen). - Der Ornithologische Beobachter 91: 73–110.
- Townsend, C. R., Scarsbrook, M. R. and Dolédec, S. 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. - Limnology and Oceanography 42: 938–949.
- Tye, A. 1992. Assessment of territory quality and its effects on breeding success in a migrant passerine, the Wheatear *Oenanthe oenanthe*. - Ibis 134: 273–285.
- Venables, W. N. and Ripley, B. D. 2002. Mass.
- Verner, J. and Ritter, L. V. 1985. Hourly Variation in Morning Point Counts of Birds (American Ornithologists' Union, Ed.). - The Auk 103: 117–124.
- ViaDonau 2016a. Doris. doris.bmvit.gv.at.
- ViaDonau 2016b. viadonau.org.
- Wagenmakers, E.-J. and Farrell, S. 2004. AIC model selection using Akaike weights. - Psychonomic Bulletin & Review 11: 192–196.
- Willson, M. F. 1974. Avian Community Organization and Habitat Structure. - Ecology 55: 1017–1029.

6. Appendix:



Appendix 1. Correlation of potential predictor variables for the GLM analysis.

Appendix 2. GLM Selection spMax based on the *AICc* (one row equals one model). The dependent variable is the spMax (log). Represented values are the degrees of freedom (*df*), the *AICc*, *AICc* weight, *p*-value and $\Delta AICc$. Included independent variables are: a = distance to water (log), b = distance to open land (log), c = deadwood (log), d= forest age, e = canopy height, f = alder (arcsin), g = ash (arcsin) and h = white poplar (arcsin) and I canopy diversity. Displayed are all models with a $\Delta AICc$ of ≤ 5 ; highlighted are the models with a $\Delta AICc$ of ≤ 2 , which are represented in the results.

Included variables	<i>df</i>	<i>AICc</i>	<i>AICc</i> weight	<i>p</i>	$\Delta AICc$
a i h f	4	-32.70	0.04	0.0063	0.00
a i f	3	-32.38	0.03	0.0083	0.32
a d f	3	-32.10	0.03	0.0094	0.60
a f	2	-31.98	0.03	0.0101	0.72
a h f	3	-31.68	0.02	0.0115	1.02
a d i f	4	-31.45	0.02	0.0109	1.25
a d h f	4	-31.21	0.02	0.0121	1.49
a d i h f	5	-31.14	0.02	0.0101	1.56
a i h g f	5	-31.04	0.02	0.0105	1.66
a i h	3	-30.99	0.02	0.0157	1.71
a	1	-30.96	0.02	0.0140	1.74
a h	2	-30.95	0.02	0.0170	1.75
a d	2	-30.93	0.02	0.0172	1.77
d f	2	-30.85	0.01	0.0179	1.85
i h f	3	-30.66	0.01	0.0183	2.04
d h f	3	-30.58	0.01	0.0190	2.12
a i	2	-30.45	0.01	0.0218	2.25
a b i h f	5	-30.45	0.01	0.0134	2.25
a e i h f	5	-30.41	0.01	0.0135	2.28
a d h	3	-30.35	0.01	0.0211	2.35
h f	2	-30.29	0.01	0.0237	2.41
a e i f	4	-30.20	0.01	0.0188	2.50
a e d f	4	-30.20	0.01	0.0188	2.50
a i g f	4	-30.18	0.01	0.0189	2.52
a b i f	4	-30.17	0.01	0.0190	2.53
a d g f	4	-30.08	0.01	0.0197	2.62
a e f	3	-30.04	0.01	0.0242	2.66
a b d f	4	-30.04	0.01	0.0201	2.66
a b f	3	-29.91	0.01	0.0257	2.79
a d i h g f	6	-29.88	0.01	0.0128	2.82
d i h f	4	-29.85	0.01	0.0217	2.85
a g f	3	-29.81	0.01	0.0270	2.89
a d i	3	-29.65	0.01	0.0290	3.05
a e h f	4	-29.63	0.01	0.0239	3.07
f	1	-29.61	0.01	0.0303	3.09
a d h g f	5	-29.61	0.01	0.0188	3.09
a h g f	4	-29.59	0.01	0.0243	3.11
a b h f	4	-29.58	0.01	0.0244	3.12
d i f	3	-29.54	0.01	0.0304	3.16
a d i h	4	-29.53	0.01	0.0249	3.17
a d i g f	5	-29.48	0.01	0.0198	3.22
a e d i f	5	-29.28	0.01	0.0215	3.42
a b d i f	5	-29.23	0.01	0.0219	3.47
i f	2	-29.22	0.01	0.0403	3.48
a e d h f	5	-29.20	0.01	0.0222	3.50

a	b	d	h	f	5	-29.11	0.01	0.0230	3.59	
a	e	d			3	-29.05	0.01	0.0379	3.65	
a	e				2	-29.04	0.01	0.0441	3.66	
a	b	d			3	-29.04	0.01	0.0381	3.66	
a	b				2	-29.03	0.01	0.0444	3.67	
a	b	h			3	-29.01	0.01	0.0387	3.69	
a	g				2	-28.97	0.01	0.0458	3.73	
a	e	h			3	-28.94	0.01	0.0400	3.76	
d	h	g	f		4	-28.93	0.01	0.0321	3.77	
a	b	i	h		4	-28.90	0.01	0.0325	3.80	
a	i	h	g		4	-28.86	0.01	0.0330	3.83	
e	d	f			3	-28.86	0.01	0.0414	3.84	
a	b	d	i	h	f	6	-28.86	0.01	0.0190	3.84
a	e	d	i	h	f	6	-28.83	0.01	0.0192	3.87
d	g	f			3	-28.79	0.01	0.0428	3.91	
a	h	g			3	-28.78	0.01	0.0429	3.92	
a	e	i	h		4	-28.78	0.01	0.0342	3.92	
a	b	i	h	g	f	6	-28.78	0.01	0.0196	3.92
i	h	g	f		4	-28.76	0.01	0.0345	3.94	
a	d	g			3	-28.75	0.01	0.0434	3.95	
a	e	i	h	g	f	6	-28.68	0.01	0.0203	4.02
b	d	f			3	-28.67	0.01	0.0450	4.03	
b	i	h	f		4	-28.50	0.00	0.0384	4.20	
e	d	h	f		4	-28.50	0.00	0.0384	4.20	
a	b	d	h		4	-28.43	0.00	0.0396	4.27	
d	h				2	-28.42	0.00	0.0604	4.28	
e	i	h	f		4	-28.42	0.00	0.0398	4.28	
d	i	h	g	f	5	-28.41	0.00	0.0304	4.29	
a	b	i			3	-28.40	0.00	0.0508	4.30	
a	e	d	h		4	-28.36	0.00	0.0407	4.34	
a	e	i			3	-28.35	0.00	0.0520	4.35	
b	d	h	f		4	-28.33	0.00	0.0412	4.36	
a	i	g			3	-28.32	0.00	0.0526	4.37	
a	d	h	g		4	-28.32	0.00	0.0415	4.38	
h					1	-28.27	0.00	0.0671	4.43	
e	h	f			3	-28.18	0.00	0.0561	4.52	
h	g	f			3	-28.18	0.00	0.0562	4.52	
a	b	e	d	f	5	-28.15	0.00	0.0337	4.55	
a	e	d	g	f	5	-28.13	0.00	0.0339	4.57	
b	h	f			3	-28.13	0.00	0.0575	4.57	
d					1	-28.11	0.00	0.0740	4.59	
a	b	e	i	h	f	6	-28.10	0.00	0.0253	4.60
a	b	d	g	f	5	-28.02	0.00	0.0354	4.68	
a	b	e	f		4	-27.95	0.00	0.0484	4.75	
a	b	e	i	f	5	-27.94	0.00	0.0366	4.76	
a	e	i	g	f	5	-27.93	0.00	0.0367	4.77	
a	b	i	g	f	5	-27.91	0.00	0.0369	4.79	
a	e	g	f		4	-27.80	0.00	0.0515	4.90	

Appendix 3. GLM Selection SDI based on the *AICc* (one row equals one model). The dependent variable is the SDI_{max}. Represented values are the degrees of freedom (*df*), the *AICc*, *AICc* weight, *p*-value and $\Delta AICc$. Included independent variables are: a = distance to water (log), b = distance to open land (log), c = deadwood (log), d= forestage, e = canopy height, f = alder (arcsin), g = ash (arcsin) and h = white poplar (arcsin). Displayed are all models with a $\Delta AICc$ of ≤ 5 ; highlighted are the models with a $\Delta AICc$ of ≤ 2 , which are represented in the results.

Included variables					<i>df</i>	<i>AICc</i>	<i>AICc</i> weight	<i>p</i>	$\Delta AICc$
h	f	c			3	-58.12	0.09	0.0015	0.00
d	h	f	c		4	-56.68	0.04	0.0028	1.44
a	h	f	c		4	-56.58	0.04	0.0029	1.54
h	g	f	c		4	-56.18	0.03	0.0035	1.94
b	h	f	c		4	-55.98	0.03	0.0038	2.14
e	h	f	c		4	-55.88	0.03	0.0040	2.24
h	f				2	-55.70	0.03	0.0046	2.43
f	c				2	-55.61	0.03	0.0048	2.51
d	h	g	f	c	5	-55.14	0.02	0.0046	2.98
d	f	c			3	-55.06	0.02	0.0064	3.06
a	d	h	f	c	5	-54.91	0.02	0.0051	3.22
h	c				2	-54.84	0.02	0.0071	3.28
a	f	c			3	-54.76	0.02	0.0074	3.36
a	h	g	f	c	5	-54.66	0.02	0.0057	3.47
a	b	h	f	c	5	-54.60	0.02	0.0058	3.53
b	d	h	f	c	5	-54.52	0.01	0.0060	3.61
e	d	h	f	c	5	-54.38	0.01	0.0064	3.74
a	e	h	f	c	5	-54.28	0.01	0.0067	3.85
a	h	c			3	-54.23	0.01	0.0095	3.90
a	h	f			3	-54.09	0.01	0.0101	4.03
b	h	g	f	c	5	-54.02	0.01	0.0074	4.10
b	h	f			3	-53.98	0.01	0.0106	4.14
d	h	f			3	-53.93	0.01	0.0109	4.19
e	h	g	f	c	5	-53.87	0.01	0.0079	4.25
a	d	f	c		4	-53.75	0.01	0.0102	4.37
b	e	h	f	c	5	-53.67	0.01	0.0086	4.45
h	g	f			3	-53.65	0.01	0.0124	4.48
e	h	f			3	-53.62	0.01	0.0126	4.51
g	f	c			3	-53.47	0.01	0.0135	4.66
b	f	c			3	-53.45	0.01	0.0136	4.68
e	f	c			3	-53.43	0.01	0.0137	4.69
d	h	c			3	-53.38	0.01	0.0141	4.75
a	d	h	g	f c	6	-53.35	0.01	0.0075	4.77

Appendix 4. GLMs of spMax (log) and sdiMax with all potential significant environment variables (distance to water (log), distance to open land (log), canopyheight, forest age, canopydiversity, proportions of white poplar, ash and alder (arcsin) and deadwood volume (log). Model names are highlighted. Given are the values estimate, Standard Error, *t*- and *p*-value.

Model / Independent variable	<i>Est.</i>	<i>SE</i>	<i>t</i>	<i>p</i>
glm_{sp}Max				
(Intercept)	3.16	0.36	8.83	<0.0001
distance to water	-0.07	0.04	-1.94	0.0564
distance to openland	-0.01	0.04	-0.21	0.8368
canopyheight	0.00	0.01	-0.12	0.9059
forest age	0.00	0.00	1.35	0.1823
canopydiversity	-0.02	0.02	-1.54	0.1285
white poplar	-0.09	0.06	-1.56	0.1228
ash	-0.08	0.07	-1.17	0.2457
alder	0.93	0.43	2.19	0.0325
deadwood	-0.02	0.01	-1.64	0.1052
glm_{sdi}Max				
(Intercept)	3.32	0.30	11.17	<0.0001
distance to water	-0.04	0.03	-1.18	0.2414
distance to openland	-0.02	0.04	-0.47	0.6381
canopyheight	0.00	0.00	0.20	0.8414
forest age	0.00	0.00	0.48	0.6316
canopydiversity	-0.03	0.01	-2.31	0.0244
white poplar	-0.12	0.05	-2.48	0.0158
ash	-0.07	0.06	-1.21	0.2328
alder	0.95	0.35	2.68	0.0093
deadwood	-0.02	0.01	-2.35	0.0220