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„Wintering birds in floodplain forests – Effects of vegetation structure and landscape composition on species assemblages"

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# Content

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# Abstract

This study explores the wintering bird community of floodplain forests in the National Park Donau-Auen. Most bird studies are conducted on breeding bird communities, but winter season can be equally important for shaping bird communities. Through 10-minute point counts, conducted between December 2015 and February 2016, bird assemblages were recorded and vegetation parameters were estimated. The number of mistletoes was very important for species richness and diversity, indicating it as a major winter food source and possible hideout. The proportion of grey alder in the canopy layer was a significant predictor for species richness as well, possibly because alder seeds remain on the tree in winter and provide a reliable food source for many bird species. Aquatic insects seem not to be an important winter food source. The amount of deadwood and forest age were not significant but deadwood showed a negative effect on bird species richness and diversity. Deadwood might be an indicator for monotonous stands which were intensively used in former forestry. Distance to open land significantly influenced bird diversity too, a higher diversity was observed on the forest`s edge. Our results suggest that in winter, food availability is the strongest factor in shaping the bird community. It seems likely too, that in the floodplain forest of the National Park Donau-Auen, habitat preferences of various bird species are stronger developed in winter than in spring. Due to the higher amount of alder trees and mistletoes in the softwood forest, a clear separation between softwood and hardwood forest bird species composition in winter appears, showing once more the importance of intact floodplain forests for bird communities.

Keywords: bird species diversity, European mistletoe, vegetation structure, National Park Donau-Auen, riparian forest, winter

# Zusammenfassung

Diese wissenschaftliche Arbeit untersucht die Wintervogelgemeinschaft von Auwäldern im Nationalpark Donau-Auen. Die meisten Studien erforschen Brutvogelgemeinschaften, obwohl die Winterperiode ebenso wichtig für die Zusammensetzung der Vogelgemeinschaften sein kann. Mithilfe von 10-minütigen Punktzählungen, durchgeführt zwischen Dezember 2015 und Februar 2016, wurde die Wintervogelgesellschaft erfasst, zusätzlich wurden Vegetationsparameter erhoben. Die Mistel Anzahl war sehr wichtig für Artenreichtum und Diversität, daraus lässt sich schließen, dass Misteln eine wichtige Nahrungsquelle darstellen und möglicherweise Versteckmöglichkeiten im Winter bieten. Der Anteil an Grau-Erle in der Baumschicht war ebenfalls ein signifikanter Prädiktor für Artenreichtum, wahrscheinlich, weil die Erlensamen im Winter am Baum bleiben und somit eine verlässliche Nahrungsquelle für viele Vogelarten darstellen. Die Menge an Totholz und das Waldalter waren nicht signifikant. Jedoch zeigt Totholz einen negativen Effekt auf die Artenzahl und Diversität der Vögel. Totholz könnte ein Indikator für monotone Flächen sein die früher intensiv forstwirtschaftlich genutzt wurden. Die Distanz zu Offenland beeinflusste ebenfalls die Vogel Diversität signifikant, eine höhere Diversität ließ sich am Waldrand feststellen. Unsere Ergebnisse deuten darauf hin, dass im Winter Nahrungsverfügbarkeit der wichtigste Faktor für die Gestaltung von Vogelgemeinschaften ist. Es ist wahrscheinlich, dass in den Flussauen des Nationalpark Donau-Auen, Habitatpräferenzen von verschiedenen Vogelarten im Winter stärker ausgeprägt sind als im Frühling. Aufgrund der höheren Anzahl von Grau-Erle und Misteln in der Weichholzau, kommt es zu einer klaren Trennung zwischen der Vogelartenzusammensetzung in der Hartholz- und Weichholzau im Winter. Dies zeigt einmal mehr die Wichtigkeit von intakten Flussauen für Vogelgemeinschaften.

Stichwörter: Vogelarten Diversität, Weißbeerige Mistel, Vegetationsstruktur, Nationalpark Donau-Auen, Auwald, Winter

# Introduction

Humans were always fascinated with the rich bird life. The millennium old dream of mankind to fly like a bird, made it as the saga of Daedalus and Icarus even into Greek mythology. But this taxonomical group has more to offer. It is more than the descendant of ancient dinosaurs with colorful representatives. Birds are important seed dispersers, pollinators, predators of insects (Bezzel & Prinzinger 1990; Wenny 2000) and ecosystem engineers (Jones et al. 1994). They can provide valuable ecosystem services for humans (Whelan et al. 2008). Some avian species are important indicators for environmental changes (Müller 2005; Utschick et al. 2012; Trautmann 2013) and represent keystone species for many ecosystems worldwide (Schaefer 2012). Attractive, prominent bird species can even act as flagship species in nature conservation (Schaefer 2012). However, in the last decades, the number of birds and bird species diversity declined worldwide. In Austria the numbers of farmland birds as well as forest birds are decreasing even though conservation measures are taking place currently (Uhl et al. 2015; Wichmann et al. 2015). For better protection and management strategies, it is crucial to understand the biology and behavior of birds as well as the ecological mechanisms which shape bird assemblages in nature.

Several studies are dealing with the effects of forest management on bird communities of Central European floodplain forests (Machar 2012). It is already known, that tree species composition can influence the structure of avian communities (Gabbe et al. 2002). Vegetation parameters such as height of canopy, shrub layer, successional stage and age class of stands can determine the occurrence of birds in forests (Donald et al. 1997; Gabbe et al. 2002; Archaux & Martin 2009; Batáry et al. 2014). However, most of bird studies are conducted during spring season when migratory birds already arrived in their breeding area. Few studies include the winter bird community (Manuwal & Huff 1987). Large differences are existing between breeding and wintering bird communities, therefore it is important to look which parameters influence the bird assemblages in winter (Cody 1973; Donald et al. 1997). Hence, this study aimed detecting vegetation and landscape parameters which are responsible for shaping bird assemblages in a lowland riparian forest in winter. Furthermore, we want to propose management recommendations.

Summer woodland bird communities in the temperate climate zone consist of resident species as well as long- and short-distance migrants. Wintering communities of the northern temperate zone contain only resident species and wintering guests from further north. It is hardly surprising that avian communities in winter react differently to environmental gradients than spring communities do (Donald et al. 1997). For many avian species winter mortality rates are high, therefore winter is a critical time period for the entire population size (Jansson et al. 1981; Donald et al. 1997; Gunnarsson et al. 2005). Resident bird species adapt to harsh winter conditions by changing their behavior (Newton 1998). For example, it is known that temperature as well as snow cover affect bird activity (Renner et al. 2012). Almeida & Granadeiro (2000) discovered, that in winter even the niche breadth of many bird species get expanded to compensate for decreased food availability. Shorter days restrict the time for foraging, snow cover reduces food accessibility and in general food is limited in quantity and quality (Jansson et al. 1981; Brotons 1997). Birds join mobile conspecific or mixed species flocks for foraging in the non-breeding season and they enlarge their home range (Matthysen 1999; Nakamura & Shindo 2001) instead of occupying and defending territories. Many resident species change their foraging behavior and become wholly or partially granivorous (Donald et al. 1997) due to the lack of invertebrates (Jansson et al. 1981). Even survival rates, time of egg-laying and breeding success can be determined by winter food availability (Jansson et al. 1981; Robb et al. 2008). But food shortage in winter might not always occur and may not be the most important factor in community structuring (Almeida & Granadeiro 2000).

During the last century river regulation and channelization occurred worldwide. Restricting streams and rivers into straight channels changes not only the fluvial geomorphic process and flood flow regime, but also alters the floodplain vegetation (Bravard et al. 1997; Arnaud-Fassetta 2003), hence leading to the loss of ecological integrity of river landscapes and declining biodiversity (Ward & Tockner 2001). Nevertheless, European floodplain forests are still highly dynamic, productive ecosystems, representing biodiversity hotspots for their region (Ward et al. 1999; Figarski & Kajtoch 2015), comparable with tropical rainforests. Sadly, today they are as endangered as rainforests (BROZ no date). Floodplain forests in general belong to the most threatened forest ecosystems worldwide (Dynesius & Nilsson 1994). Most of regularly flooded, alluvial forests in Central Europe have become reduced to tiny fragments as a result of river regulation (Flade 2001). The extinction risk in fragmented landscapes is significantly higher than in undisturbed environments (Fahrig & Merriam 1985), showing clearly the importance of intact floodplain forests as dispersal corridors for many biological groups (Lees & Peres 2008). In Austria only 15% of original floodplain forests remain (Naturschutzbund Österreich n.d.; Lazowski & Schwarz 2015).

The intermediate disturbance hypothesis (Connell 1978), the patch-corridor-matrix model (Forman 1995) and the ecotone concept (Naiman & Decamps 1990; Risser 1995) account for the importance of intact river landscapes and explain their high biodiversity. River landscapes are characterized and strongly influenced by flooding events, leading to intermediate disturbances which create a mosaic of different successional stages. Organisms of early and late successional stages can coexist on small spatial scales, which leads to a high species richness (Ward et al. 1999; 2001). Intact riparian forests are essential for maintaining the diversity of plant and animal communities in many biomes. Alluvial forests are escorting rivers over long distances and can be seen as important dispersal corridors for woodland organisms, making it possible for these organisms to migrate into other biomes and inhabit new habitats in an otherwise fragmented landscape (Silva 1996). Through enhanced connectivity between isolated habitat patches, the number of successfully dispersing individuals rises. Thus, the genetic variability increases and the risk of local extinctions decreases (Lees & Peres 2008; Vieira & Carvalho 2008; Figarski & Kajtoch 2015). A negative result of enhanced connectivity is the fast spread of invasive species along river systems and adjacent forests, making it very difficult to stop their spatial expansion (Essl & Rabitsch 2002).

The Danube is the second largest and longest river in Europe, flowing through 10 countries and its river basin extending to 19 countries.
The Danube and its tributaries with their riparian forest connect Continental Europe with the Black Sea and it is an important corridor for animal and plant migration (Jungwirth et al. 2014; Figarski & Kajtoch 2015). In the 19$^{th}$ century, river regulation measures were made along the Danube resulting in the channelization of the river. Only four short, free flowing

sections on the upper reaches are left nowadays, one of them is located at the National Park Donau-Auen east of Vienna, where our study was conducted.

However, the river landscape east of Vienna changed immensely during the last century due to human activities. Logging, damming for flood protection and destruction of floodplain forests for land reclamation as well as the introduction of neophytic species changed the forest characteristics. Regulating the Danube and damming most of its side arms changed its hydrological dynamic and caused the side arms to silt up. As a result, the vegetation and habitat structure was altered (Schratt-Ehrendorfer 2000; Jungwirth et al. 2014). Nowadays a fundamental rethinking in Austria has started, leading to various river restoration projects. Also in the National Park Donau-Auen river bank restoration and side arm reconnection projects were implemented recently (Nationalpark Donau-Auen no date 1; Jungwirth et al. 2014).

The aim of this study was to identify vegetation and landscape parameters which influence the composition and diversity of wintering bird assemblages in floodplain forests in the Donau-Auen National Park. Further, we analyzed to what extent food availability is shaping wintering bird communities in the National Park Donau-Auen. Especially mistletoe occurence might highly influence species richness and diversity because mistletoe berries ripen in winter and therefore provide a reliable food source for many fruit-feeding bird species (Nierhaus-Wunderwald & Lawrenz 1997).
We also considered if plots near water bodies contain higher bird diversity and a higher species richness than plots further away. Some studies already confirmed for spring season, that, due to increased insect abundance near water bodies, insectivorous bird species (Iwata et al. 2003) and bird species richness increases (Adrion 2016). Plots near water bodies may contain more (aquatic) insects even in winter season, therefore providing an important additional winter food source. We also expect a higher species richness and diversity on plots with a high amount of standing deadwood and bigger deadwood volume. Especially insectivorous bird species benefit from a high amount of deadwood because of higher prey availability. Cavities in deadwood might additionally provide good hideouts and weather protection (Nilsson 1979).

# Materials and methods

## Study area

The study was conducted in a lowland floodplain forest in the National Park Donau-Auen, east of Vienna, in the federal state of Lower Austria between December 2015 and February 2016. The national park was established in 1996 and stretches from Vienna, Austria to the Slovakian border. It contains not only the longest free flowing section of the Danube in Austria but also the biggest semi-natural floodplain forests in Central Europe. There is no commercial logging in the national park, in some parts management measures (e.g. mowing of pastures, removal of neophytes) take place. The area consists of a network of riparian forest (65%), water bodies (20%) and meadows (15%) (Nationalpark Donau-Auen no date 2; Manzano 2000). The Riverine Wetland National Park Donau-Auen is acknowledged by the IUCN, Category 2, since 1997. Furthermore, the area is a UNESCO Biosphere Reserve, a Ramsar Wetland Area and a Natura 2000 Site according to the Flora-Fauna-Habitats Directive (Nationalpark Donau-Auen no date 2; Umweltbundesamt no date; Dvorak & Karner 1995).

The National Park Donau-Auen is located at the eastern edge of the Pannonian floral province and is therefore situated in the Pannonian region, implying Pannonian climate conditions, such as warm and dry summers and low annual precipitation rates (Fischer & Mazzucco 2011). The national park covers an area situated between 140 and 150 meters above sea level (Land Niederösterreich 2017).

Since the beginning of the recording in 1768, 2015 was the second warmest year in Austria. Furthermore, the winter 2015-2016 was the second warmest winter since the last 250 years. Especially in Lower Austria the annual precipitation level was lower than in average, resulting in snow deficit (ZAMG 2016). Due to extraordinary hot and dry weather conditions in 2015 almost all "permanent" waterbodies in our study area ran dry before fieldwork started. For our study area, no precipitation data are available, but the three closest weather stations measured 398 mm (Schwechat), 450 mm (Groß-Enzersdorf) and 565 mm (Bad Deutsch-Altenburg) rainfall for the year 2015. The average annual precipitation recorded at these weather stations between the years 1971 and 2000 was around 501 and 750 mm. The average annual temperature was between 8 and 10 °C. In the year 2015 the average annual temperature in Schwechat was 11.6 °C, in Groß-Enzersdorf 11.8 °C and in Bad Deutsch-Altenburg 11.8 °C (ZAMG no date 1).

In Austria, the Danube is a mountain river still in its upper reaches (Schratt-Ehrendorfer 2011; Jungwirth et al. 2014). The historic Danube was gravel-dominated and a laterally active anabranching river, meaning that it showed attributes from a branched as well as a meandering river (Nanson & Knighton 1996). Today the Danube flows as a straightened main channel through Austria due to implemented river regulation measures. Only at two sites (at the National Park Donau-Auen and in the Wachau) the Danube still shows its furcation characteristics, implying that it is a branched river containing gravel banks as well as naked and overgrown islands (Jungwirth et al. 2014). Flooding events occur most frequently in early summer due to snowmelt at higher altitudes in the Alps. However, floods can occur the entire year due to heavy rainfall. Winter floods through ice dam formations occur infrequently but can be severe (Manzano 2000; Schratt-Ehrendorfer 2011; Jungwirth et al. 2014).

In the 19th century a dam was built at the northern shore of the Danube east of Vienna to protect the lowland plain Marchfeld and its villages from floods. This flood protection dam, called “Marchfeldschutzdamm” in Lower Austria and “Hubertusdamm” in Vienna, divides the floodplain area into a regularly flooded territory south of the dam and a northern territory which is disconnected from the natural flood dynamic of the Danube. At the dammed-up area a fast succession from softwood to hardwood forest is taking place, making it possible to find tree species from softwood and hardwood riparian forest together at the same place. For dotation measures the “Schönauer Schlitz” remains as the only passage where Danube water is allowed to enter the riparian forest at high water (Schratt-Ehrendorfer 2000).

## Study site selection

The census points used for assessing bird assemblages were located north and south of the “Marchfeldschutzdamm” between Schönau (48°14’ N, 16°61’ E) in the west and Stopfenreuth (48°14’ N, 16°88’ E) in the east. The furthest distance between census points was 25 km. Selected census points were identical to the ones used by Adrion (2016), who assessed breeding bird assemblages of floodplain forests in spring 2015. These points are located at the intersection of 100 m grids established by the Österreichische Bundesforste AG and the MA 49 of Vienna in the framework of their forest inventory scheme. These points were filtered with ArcMap 10.2 (ESRI 2011) for the following criterias: (1) max. 100 m away from paths (for good accessibility); (2) no forest margin within a 50 m radius; (3) >200 m apart from other points (for spatial independency). Further, the plots were grouped by distance to next permanent water bodies using the following categories: <75 m, 75-150 m, 150-250 m and >250 m. For every distance class, 25 points were chosen randomly (Adrion 2016). Subsequently, points closely located to nesting sites of Eastern Imperial Eagles *(Aquila heliaca)* and White-tailed Eagles *(Haliaeetus albicilla)* were excluded to reduce human disturbance. This selection resulted in a total of 72 remaining census points used in the study of Adrion (2016). Three plots were deforested before or during our fieldwork, hence in total 69 plots remained for this study (Figure 1).

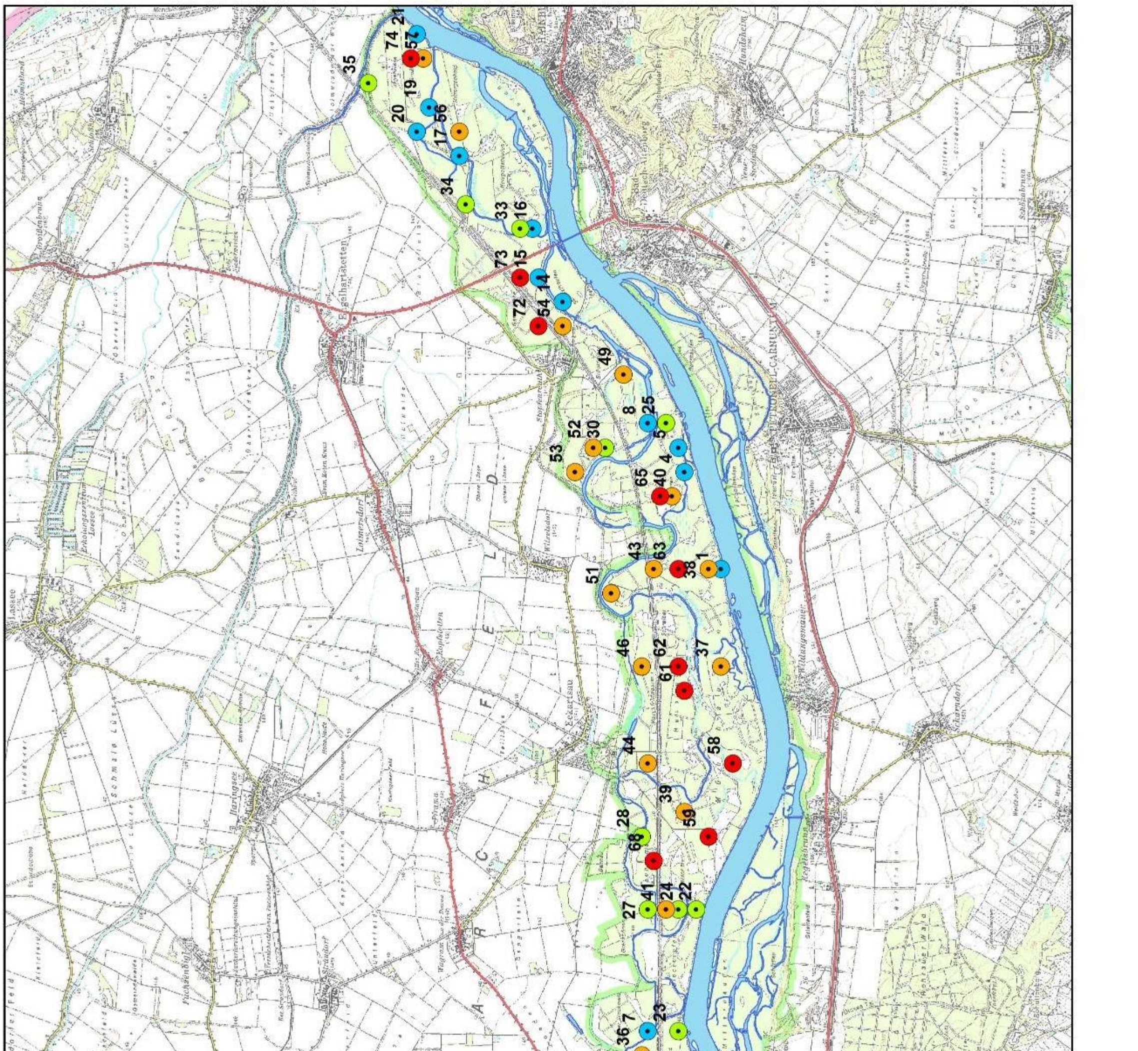


*Figure 1 Surrounding map of the National Park Donau-Auen. Census points are marked and labelled according to their distance class to permanent water bodies*

## Bird counts

Every census point was visited once a month between December 2015 and February 2016, resulting in three visits per site. The order of visits was changed between the survey rounds. In winter, bird activity is lower and detection is harder than in other seasons. But even in winter birds are more active in the morning (Almeida & Granadeiro 2000). Due to this reason 10-minute point counts, as did Hutto et al. (1986), Donald et al. (1997) and Laiolo (2002; 2003) in their studies, were carried out between sunrise and 4 hours afterwards.
Local sunrise occurred between 7:24 a.m. in December and 6:37 a.m. in February (ZAMG no date 2).
The point count method (Bibby et al. 1995), recording all birds detected visually or acoustically during a pre-assigned time period (in this study: 10 min), was chosen for this study. We noted for every recorded bird, if it was outside the 50 meter radius or just overflew the plot. Such individuals were not included in further analyses because they did not utilize habitat structures of our study sites. We assumed, like Hutto et al. (1986), that bird species which were observed in a 50 m circle had a strong relationship with plot habitat characteristics. There has been no field work at bad weather conditions like high wind and heavy rain. The wind speed was estimated on the Beaufort-Scale; no point counts were conducted when wind speed reached 4 bft (moderate breeze, 20-28 km/h).

## Habitat variables

Vegetation parameters were recorded during the first visit of the census points in December 2015. Leaf litter coverage (%) were estimated as well as the maximum height of closed canopy with the help of the range finder Nikon Laser 800 6x216. All trees partly or fully covered in ivy (*Hedera helix*) as well as the number of mistletoes *(Viscum album)* were counted within a radius of 50 m around census points.
To estimate understory vegetation coverage, eight pictures were taken in different directions from the center of the census point. Every picture was separately rated into one of three categories: category 1 for poorly developed understory, meaning that only 0-25% of the area was covered with understory, category 2 (25-50 %) and category 3 for an extraordinary high coverage of understory plants (>50 %). The reference pictures are provided in Appendix 3. Understory plants include woody vegetation like bushes and shrubs as well as weeds. As measurement for understory coverage the mean of the eight pictures per point was calculated for each census point.
Furthermore, the number and species of fruiting bushes and trees were counted after a short search.
Additionally, distances of census points to permanent water bodies and open land calculated with ArcMap 10.2 (ESRI 2011) were provided by Adrion (2016). We further used the number of stems of standing deadwood with a diameter at breast height (DHB) of ≥ 10 cm counted within a radius of 20 m around census points by Waringer (2017). As also their height was measured, the deadwood volume could be calculated by simplifying the stems to a cylinder and extrapolate the volumes for the area (Waringer 2017). Forest stand data, containing tree species composition and stand age, were provided by the ÖBF and MA49.

## Statistical analysis

The statistical analysis has been conducted with PAST Version 3.10 (Hammer et al. 2001) and R Studio Version 1.0.136 (RStudio Team 2016). The following packages were used in RStudio: ape (Paradis et al. 2004), betapart (Baselga 2010), ecodist (Goslee & Urban 2007), glmulti (Calcagno 2013), PerformanceAnalytics (Peterson & Carl 2014), sp (Pebesma & Bivand 2005) and vegan (Oksanen et al. 2016).

A correlation matrix of all potential predictor variables was calculated to see the extent of correlation (see Appendix 3). All variables had a correlation coefficient below our threshold of 0.6 (Dormann et al. 2013) and were therefore available for producing generalized linear models (GLMs) and non-metric multidimensional scaling (NMDS) ordinations.

The bird dataset was not distinguished further in female, male, calling or singing birds. Birds flying over the plot or individuals detected outside the 50 m radius were never considered in any analysis.

To find important habitat and landscape parameters which influence bird assemblages, GLMs were calculated with R package glmulti. Only 68 of 69 census points were included in the GLMs and NMDS ordinations because for one plot deadwood data were missing. 15 predictor variables (see Table 1) were included as explanatory variables in the GLMs. Hybrid poplar (*Populus canadensis*) was excluded from the GLMs, as did Adrion (2016). The function "glmulti" automatically generated all possible models (33900 models for 15 predictor variables) and found the best model regarding Information Criterion (criterion AIC, level 1). The response variable for the GLM was for one model **ntax** (total number of species per plot over the three survey rounds) and for the other model **sh_birds** (Shannon Diversity Index). The ntax model accounts for species richness and the sh_birds model accounts for species diversity. The Shannon Diversity index is commonly used in ecology to describe communities because it not only takes the total species number (ntax) into account but also considers species abundance (Legendre & Legendre 2003).

We did not only consider the result of the best fitted model, but also looked at the best 100 models. The importancy of one environmental predictor increases with the weights/probabilities of the model in which the variable appears. A predictor is more important if it shows up in lots of models with large weights (Viechtbauer 2016).

To check for spatial autocorrelation the best model of ntax and sh_birds (produced by glmulti), were tested with help of the "Moran.I" function in the ape package of R. The residuals of the best models were compared with the coordinates of the census points. If spatial autocorrelation exists, the observed value of Moran's I is significantly different from the expected value. Positive autocorrelation exists if the observed value is significantly higher, negative autocorrelation exists if the observed value is significantly lower than the expected value. The graphs visualizing spatial distribution of model residuals (see Figure 5 and 6) are produced with R package sp.

To partition beta diversity into species turnover and nestedness, the framework of Baselga (2010) was used. With help of the function "beta.multi" of the R package betapart, multiple-site dissimilarities with the dissimilarity index Sørensen was calculated. The turnover rate was measured as Simpson dissimilarity, the nestedness component and overall beta diversity were both measured as Sørensen dissimilarity index.

For checking if the bird assemblage depends on tree species composition in the canopy layer, multiple regression on distance matrices (MRM, permutation= 1000) were performed. Before calculating MRM, the bird matrix was square root transformed and the Bray-Curtis distance matrix of the transformed bird matrix was calculated. An Euclidean distance matrix

was calculated for the predictor tree species composition (proportion of the four most common tree species in the canopy layer).
An ANOSIM (one-way, permutation= 9999) was run in PAST to test for differences in species composition (quantified as Bray-Curtis similarities) between bird assemblages north and south of the flood protection dam.
Furthermore, Nonmetric Multidimensional Scaling (NMDS) was performed with the function "metaMDS" of the vegan package. Only bird species which were detected at least in 10 different plots were considered, resulting in 15 used bird species in the NMDS (k=2, trymax= 1000). The bird data had been square root transformed. The NMDS is a robust, unconstrained ordination method which is the best approach when handling data with a strong community turnover or arch effect. It only needs the bird matrix for computation and afterwards fits the environmental parameters (all 16 environmental parameters were used) into the graph, allowing an optical visualization and interpretation which predictors are responsible for most of the variance in species composition.
Furthermore, bird species were categorized into one of three food guilds according to their nutrition entries from the books of Glutz von Blotzheim & Bauer (1985; 1988; 1993a; 1993b; 1994; 1997a) In the NMDS ordination shown in Figure 9 feeding guild affiliation of all considered bird species is indicated.
For statistical testing of the NMDS results, a Permanova was run with the function "adonis" (permutations= 999, method= Bray-Curtis). It tests which environmental predictors are significant and it shows the different weighting.

# Results

We observed 48 bird species with 2513 individuals in total (see Appendix 1 and 2 for details). We excluded 14 species because these were either observed only outside the 50 m radius, flew over and did not get in touch with the habitat or were water bird species. Finally, 34 species with 1934 individuals remained for all subsequent analyses. The most abundant bird species which were detected in all 69 plots were Great Tit (*Parus major*) with 568 individuals (506 individuals inside the 50 m radius) and Eurasian Nuthatch (*Sitta europaea*) with 377 individuals (303 inside). The third most abundant bird species was Blue Tit (*Cyanistes caeruleus*), which was detected at 67 census points with a total of 325 individuals (320 inside). Considering only the individuals which were detected inside the 50 m radius and are taken in account for analysis, Blue Tit is the second most abundant bird species.

## Habitat variables

Table 1 shows all 16 environmental variables which were used in our analyses.

***Table 1*** *Habitat measurements, their extremes and mean values*

| ***Code*** | ***Name*** | ***Description*** | ***Range*** | ***Mean value*** |
|---|---|---|---|---|
| leaves | Leaf litter coverage | % of ground covered with leaf litter | 30-100 | 80.58 |
| understory | Understory | % coverage of understory, organized in 3 categories (0-25%, 25-50%, 50-100%) | 1-3 | 1.64 |
| mistletoes | Mistletoes *(Viscum album)* | Number of mistletoes per plot | 0-150 | 30.75 |
| ivy | Ivy trees (*Helix hedera*) | Number of trees partly or fully covered in ivy | 0-40 | 2.3 |
| height_canopy | Max. height of closed canopy | m above ground where majority of trees have their treetop | 8-30 | 17.07 |
| nr_fruits | Fruiting trees | Number of trees and shrubs with seeds or berries | 0-20 | 3.36 |
| water | Distance to waterbodies | Distance from plot center to permanent water bodies (m) | 48-457 | |
| openland | Distance to open land | Distance from plot center to open land (m) | 51-394 | |
| c_div | Canopy diversity | Number of tree species in canopy | 1-8 | 3.17 |
| age_S1 | Mean age S1 | Mean age of trees in canopy layer in 20 m radius | 20-98 | 57.76 |
| st_dw | Standing deadwood | Number of standing deadwood in 20 m radius | 1-119 | 14.36 |
| vol_dw | Volume deadwood | Volume of all dead, standing trees in 20 m radius ($m^3$) | 3832-42715826 | 4598793.444 |
| pop_alba | White poplar *(Populus alba)* | % of white poplar in canopy layer in 20 m radius | 0-100 | 31.8 |
| pop_cana | Hybrid poplar *(Populus canadensis)* | % of hybrid poplar in canopy layer in 20 m radius | 0-97 | 8.8 |
| frax_exc. | European ash *(Fraxinus excelsior)* | % of European ash in canopy layer in 20 m radius | 0-100 | 23.44 |
| alnus_incana | Gray alder (*Alnus incana*) | % of gray alder in canopy layer in 20 m radius | 0-30 | 1.89 |

The parameter number of fruits consists of all trees and shrubs with seeds or berries found in December on the census points after a quick search. Table 2 lists all found plant species. Alder trees in the canopy layer occur only on the south side of the dam.

*Table 2 Fructiferous trees and shrubs noted, ordered by total individual numbers over the 69 census points*

| **English name** | **Scientific name** | **Range** | **Total** |
|---|---|---|---|
| Old man`s beard | *Clematis vitalba* | 0-20 | 122 |
| European ash | *Fraxinus excelsior* | 0-3 | 42 |
| Grey Alder | *Alnus incana* | 0-10 | 20 |
| Black locust | *Robinia pseudoacacia* | 0-10 | 19 |
| Hawthorn | *Crateagus* sp. | 0-3 | 17 |
| Maple | *Acer* sp. | 0-2 | 8 |
| Spindle tree | *Euonymus* sp. | 0-1 | 2 |
| Wild privet | *Ligustrum vulgare* | 0-1 | 2 |
| Guelder-rose | *Viburnum* sp. | 0-1 | 1 |

The number of mistletoes on the south side of the dam is significant higher (Kruskal-Wallis test for equal medians: $p$= 0.0083) than north of the dam (see Figure 2). A correlation chart of all environmental variables is shown in Appendix 3.

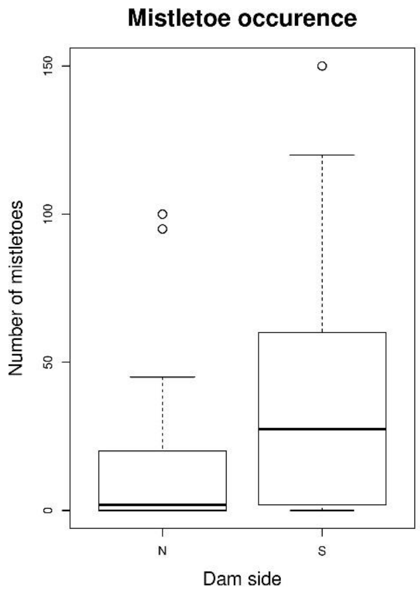


*Figure 2 Median mistletoe abundance, North side of the dam: box (0, 20), whisker (0, 45), median= 2; South side of the dam: box (2, 60), whisker (0, 120), median= 27.5*

## Species richness

The best GLM model for species richness as response variable (regarding AIC) included the explanatory variables standing deadwood, gray alder and mistletoes (see Table 3 for details). There were 16 models which had an AIC ≤ 2 (see Appendix 4, Table 12). The predictors grey alder and mistletoes were significant but the included standing deadwood was not. Figure 3 shows the proportion of the predictor variables present in the best 100 calculated models. The number of mistletoes as well as the proportion of alder in the canopy layer were included in over 80% of all models.

*Table 3 Summary of the best model of ntax, signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

| Explanatory variables | **Estimate Std.** | **SE** | ***t* value** | ***Pr* (>\|*t*\|)** |
|---|---|---|---|---|
| **Intercept** | 7.9424 | 0.4313 | 18.417 | <0.0001 *** |
| **st_dw** | -0.0247 | 0.0158 | -1.557 | 0.1243 |
| **alnus_incana** | 0.1098 | 0.0474 | 2.315 | 0.0238 * |
| **mistletoes** | 0.0230 | 0.0068 | 3.366 | 0.0013 ** |

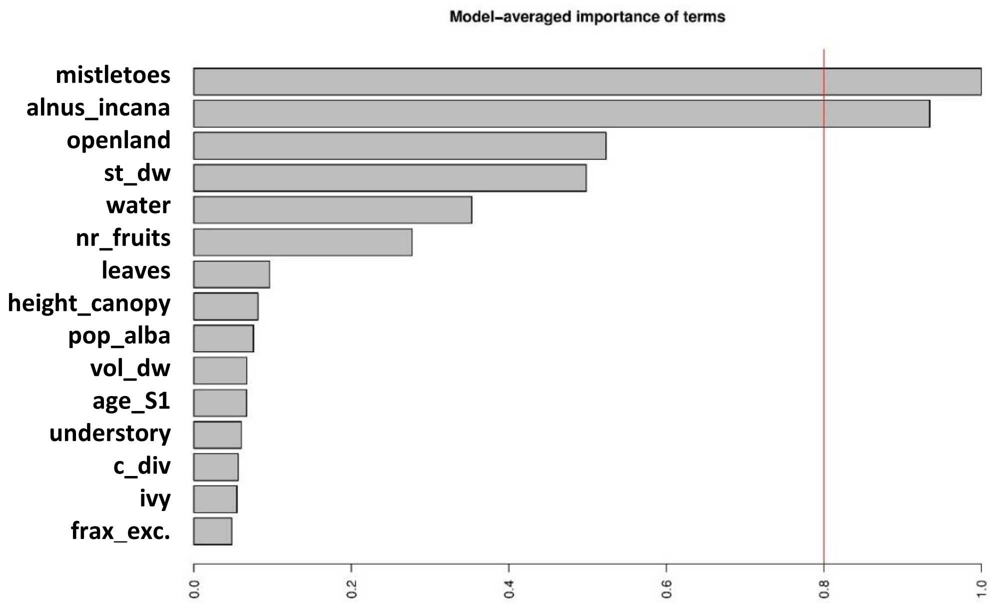


*Figure 3 Model-averaged importance of terms; red line at 80%; for abbreviations of explanatory variables compare Table 1*

## Species diversity

The best GLM model testing for effects of vegetation and landscape structure variables on bird species diversity (Shannon Diversity Index) included distance to open land, standing deadwood, proportion of grey alder in the canopy layer, number of mistletoes and number of fruits and seeds.
In this model, only open land and mistletoes proved to significantly affect bird diversity (see Table 4). There were 13 models with an AIC of ≤ 2 (see Appendix 4, Table 13). Figure 4 shows the importance of the environmental predictors for the best 100 models. The predictors mistletoe, grey alder and open land were in over 80% of the 100 best models present.

*Table 4 Summary of the best model of sh_birds, Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

| Explanatory variables | **Estimate Std.** | **SEr** | ***t* value** | ***Pr* (>\|*t*\|)** |
|---|---|---|---|---|
| **(Intercept)** | 1.8932 | 0.0472 | 40.077 | <0.0001 *** |
| **Openland** | -0.0005 | 0.0002 | -2.076 | 0.0420 * |
| **st_dw** | -0.0023 | 0.0012 | -1.827 | 0.0725 . |
| **alnus_incana** | 0.0071 | 0.0038 | 1.892 | 0.0632 . |
| **mistletoes** | 0.0028 | 0.0006 | 4.927 | <0.0001 *** |
| **nr_fruits** | 0.0101 | 0.0057 | 1.781 | 0.0798 . |

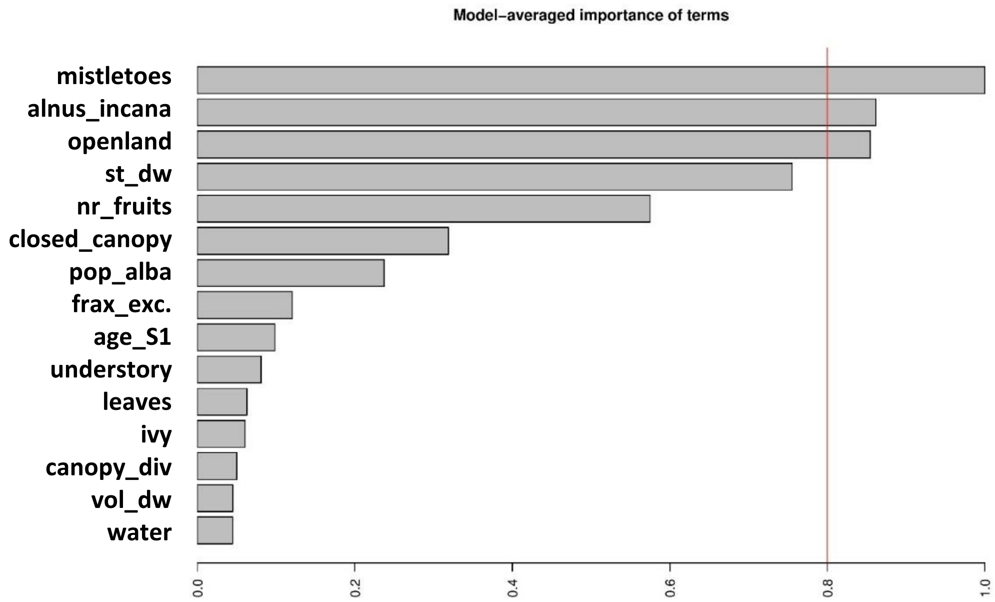


*Figure 4 Model-averaged importance of terms; red line at 80%*

## Spatial autocorrelation

For the best GLM model with bird species richness as response variable, no autocorrelation exists (see Table 5 and Figure 5). For bird species diversity as response variable, no autocorrelation was detected either (see Table 6 and Figure 6).

*Table 5 Results of function Moran.I for the residuals of the best glm model with the response variable bird species richness*

| | |
|---|---|
| **Observed** | -0.0098 |
| **Expected** | -0.0149 |
| **Standard deviation** | 0.0115 |
| ***p* value** | 0.6528 |

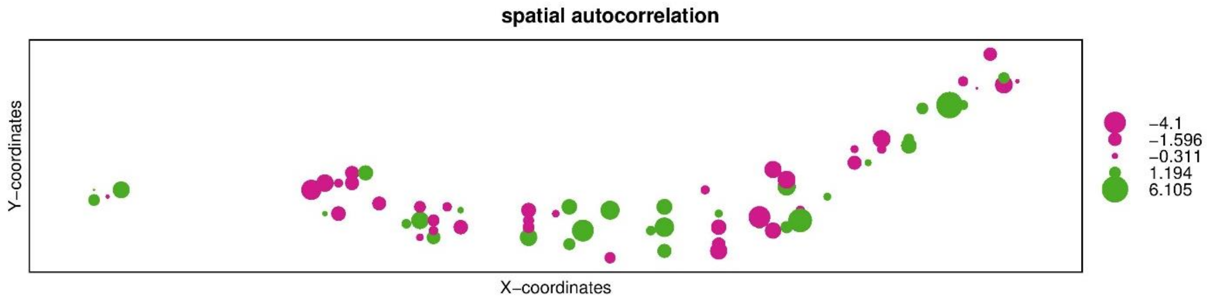


*Figure 5 Spatial distribution of positive and negative model residuals of the best model with bird species richness as response variable*

*Table 6 Results of function Moran.I for the residuals of the best model with the response variable bird species diversity*

| | |
|---|---|
| **Observed** | -0.0165 |
| **Expected** | -0.0149 |
| **Standard Deviation** | 0.0115 |
| **P value** | 0.8901 |

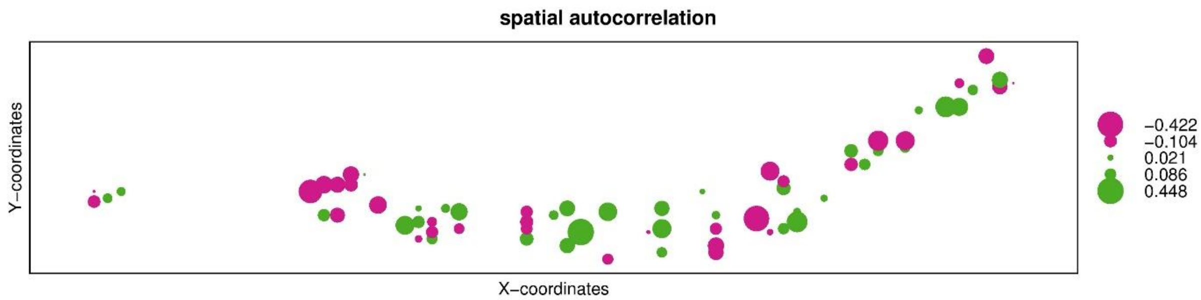


*Figure 6 Spatial distribution of positive and negative model residuals for the best model with bird species diversity as response variable*

## Species composition

With help of the betadiver package (Baselga 2010) in R Studio we were able to distinguish the beta diversity ($\beta_{SOR}$) into effects of species turnover ($\beta_{SIM}$) and nestedness ($\beta_{SNE}$).
The overall beta diversity for our 69 census points achieved a Sørensen dissimilarity of 0.93 ($\beta_{SOR}$). The spatial turnover in species, measured as Simpson dissimilarity, was mainly responsible for the recorded beta diversity ($\beta_{SIM}$= 0.89). Nestedness, measured as Sørensen dissimilarity, contributed sparsely ($\beta_{SNE}$= 0.05) to overall beta diversity.

A calculated multiple regression (MRM) on distance matrices (Euclidean distance used) for the predictor tree species and the response bird matrix (square root transformed abundances, Bray-Curtis dissimilarity used, permutations= 1000) did not indicate any relationship between the four most abundant tree species in the canopy layer (gray alder, European ash, white poplar and hybrid poplar) and bird species composition (MRM: $R^2$<0.01, $p$= 0.99).

Bird species composition differed significantly between census points north and south of the dam "Marchfeldschutzdamm" (one-way ANOSIM: $p$= 0.039).
Bird assemblages north and south of the dam are significantly different from each other and the variance within each group is smaller than between groups. Furthermore, more bird species were detected south of the dam (one-way ANOVA, p= 0.0182, see Figure 7).

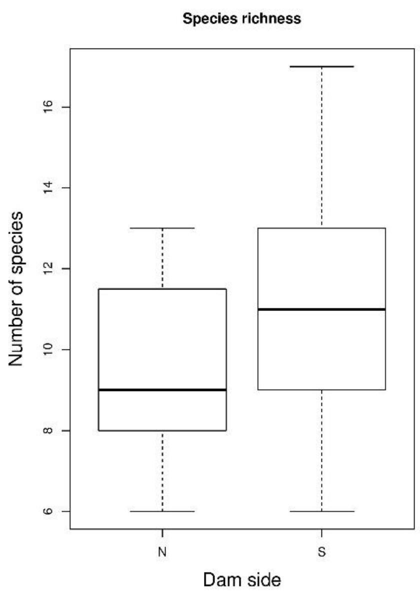


*Figure 7 Median species richness of census points north and south of the dam; North side: box (8, 11.5), whiskers (6, 13), median= 9; South side: box (9, 13), whiskers (6, 17), median= 11*

## Habitat preferences of species

We calculated an NMDS to visualize similarity relationships between census points and to analyse habitat preferences of bird species.
The environmental variables with the longest arrows are: mistletoes, age of the canopy layer, proportion of grey alder in the canopy layer, distance to open land and number of standing deadwood. Short arrows belong to ivy, number of fruits and seeds and leave litter coverage (see Figure 8). The angle of the arrow indicates the best fit of the environmental variable and shows the direction in which the values increase. The length of the arrow represents its power (high $R^2$ values for long arrows). Species and plots close together are more similar than others. Table 8 shows which environmental predictors are associated with NMDS1 and NMDS2 axes and how much variance ($R^2$) they explain. The vector mistletoes, for example, is negatively associated with axes NMDS2 and explains 35% of its variance.

*Table 7 All 16 environmental vectors associated with NMDS1 and NMDS2 axes, Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*

| | **NMDS1** | **NMDS2** | ***R*²** | ***P*r(>r)** | |
|---|---|---|---|---|---|
| **c_div** | 0.53057 | -0.84764 | 0.0589 | 0.127 | |
| **understory** | 0.27466 | -0.96154 | 0.0434 | 0.248 | |
| **pop_cana.** | -0.13781 | -0.99046 | 0.0765 | 0.063 | . |
| **height_canopy** | 0.98627 | -0.16516 | 0.0455 | 0.217 | |
| **water** | -0.26591 | 0.96400 | 0.0128 | 0.648 | |
| **openland** | -0.83498 | -0.55027 | 0.1138 | 0.018 | * |
| **age_S1** | 0.46076 | 0.88752 | 0.1186 | 0.017 | * |
| **st_dw** | -0.55046 | 0.83486 | 0.0945 | 0.039 | * |
| **vol_dw** | -0.40789 | 0.91303 | 0.0089 | 0.742 | |
| **pop_alba** | -0.68122 | -0.73208 | 0.0429 | 0.237 | |
| **frax_exc.** | -0.26598 | 0.96398 | 0.0425 | 0.247 | |
| **alnus_incana** | 0.41375 | -0.91039 | 0.1063 | 0.028 | * |
| **mistletoes** | 0.27925 | -0.96022 | 0.3530 | 0.001 | *** |
| **Ivy** | 0.35983 | 0.93302 | 0.0150 | 0.597 | |
| **nr_fruits** | 0.18215 | -0.98327 | 0.0046 | 0.881 | |
| **leaves** | -0.75974 | 0.65022 | 0.0276 | 0.421 | |

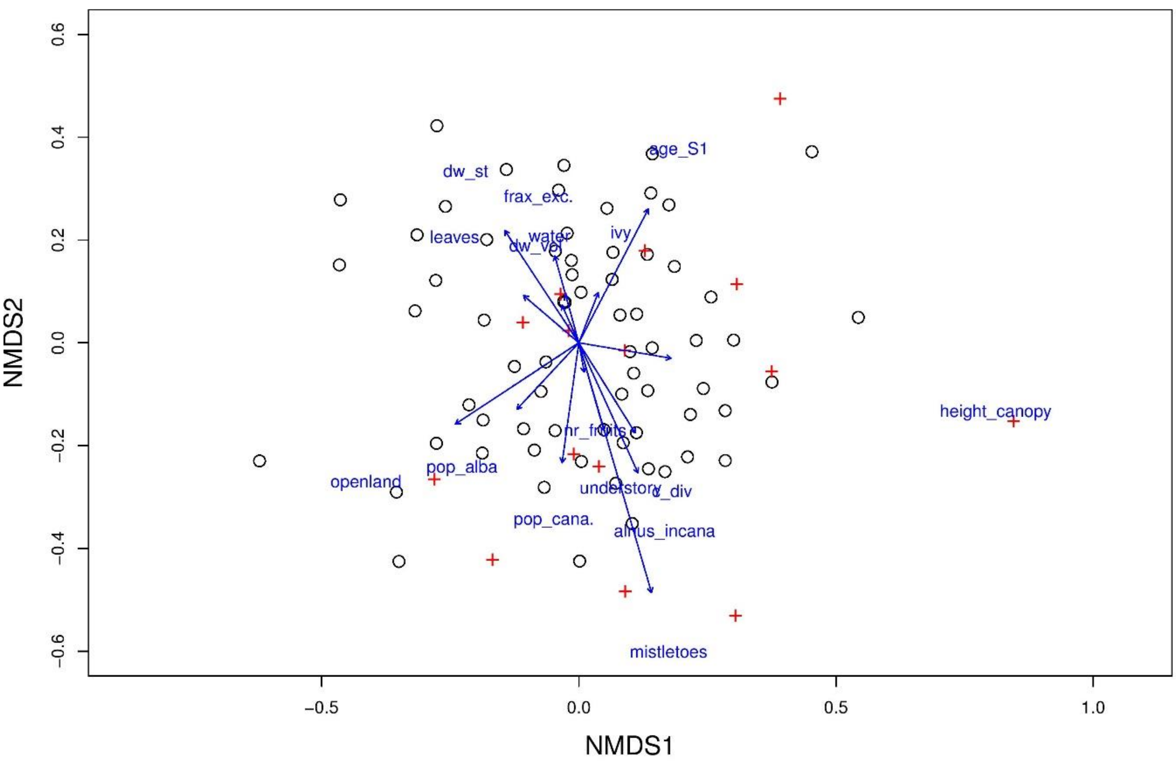


*Figure 8 NMDS plot of site data (circles) and bird species (red crosses). Environmental predictors are shown as arrows; length of arrows indicates its power. stress= 0.26.*

In the NMDS ordination shown in Figure 9 feeding guild affiliation of all considered bird species is indicated. The insectivorous guild (red circles), includes Black Woodpecker, Eurasian Treecreeper, Great Spotted Woodpecker, Long-tailed Tit and Eurasian Wren, the omnivorous guild (green circles) includes species which uses a broad range of food sources, such as Eurasian Nuthatch, Blue Tit, Great Tit, Blackbird and Eurasian Jay. The third guild (blue circles) includes bird species which exclusively or mainly feed on berries and seeds in winter, these are: Marsh Tit, Mistle Thrush, Bullfinch, Hawfinch and Chaffinch. No clear clustering can be distinguished. The calculated NMDS ordination did not indicate a preference of bird species for certain forest types related to their feeding guild affiliation.

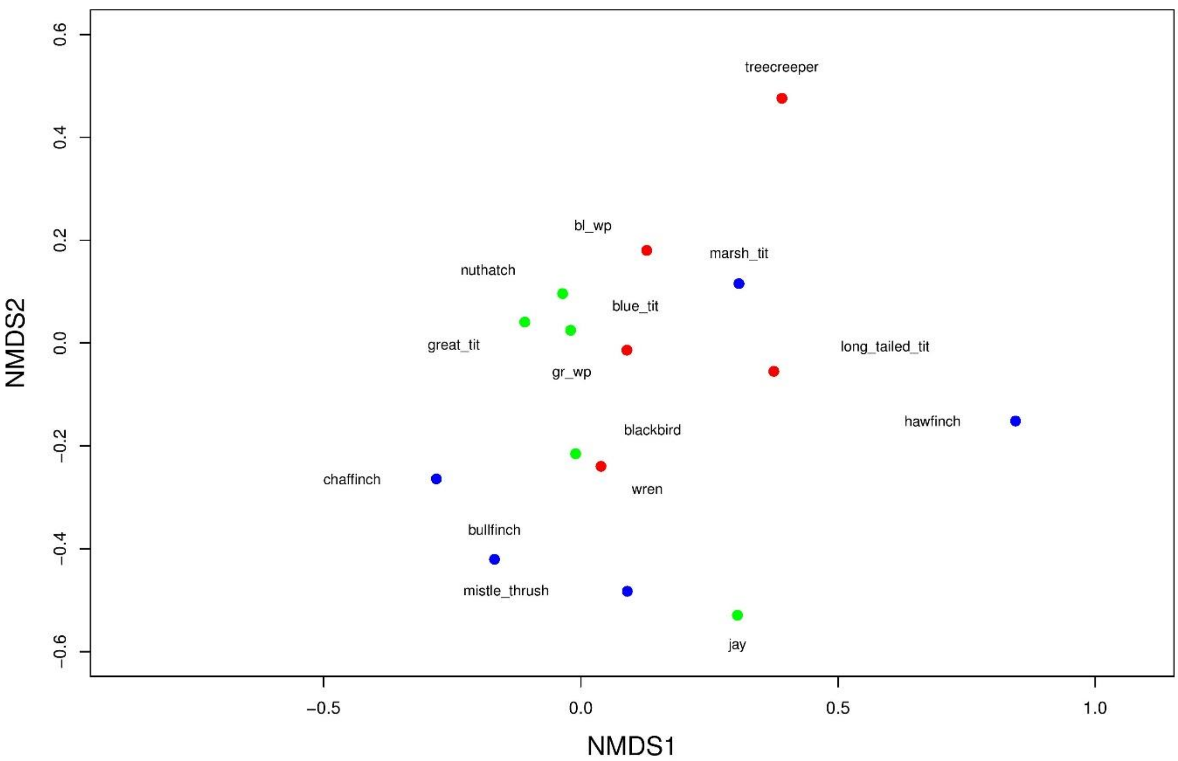


*Figure 9 NMDS plot with bird species. The color shows its membership to one of three food guilds. red= insectivore, green= omnivore, blue= ranivore; bl_wp= Black Woodpecker, treecreeper= Eurasian Treecreeper, gr_wp= Great Spotted Woodpecker*

Figure 10 shows the bird species and environmental predictors. The occurrence of Eurasian Treecreeper seems to be strongly associated with the age of the canopy layer S1. Mistle Thrush and Jay are located near the arrows of the number of mistletoes and proportion of alder in the canopy layer. Height of canopy seems to be a good predictor for Long-tailed Tit and for Hawfinch. Chaffinch seems to correlate with distance to open land.

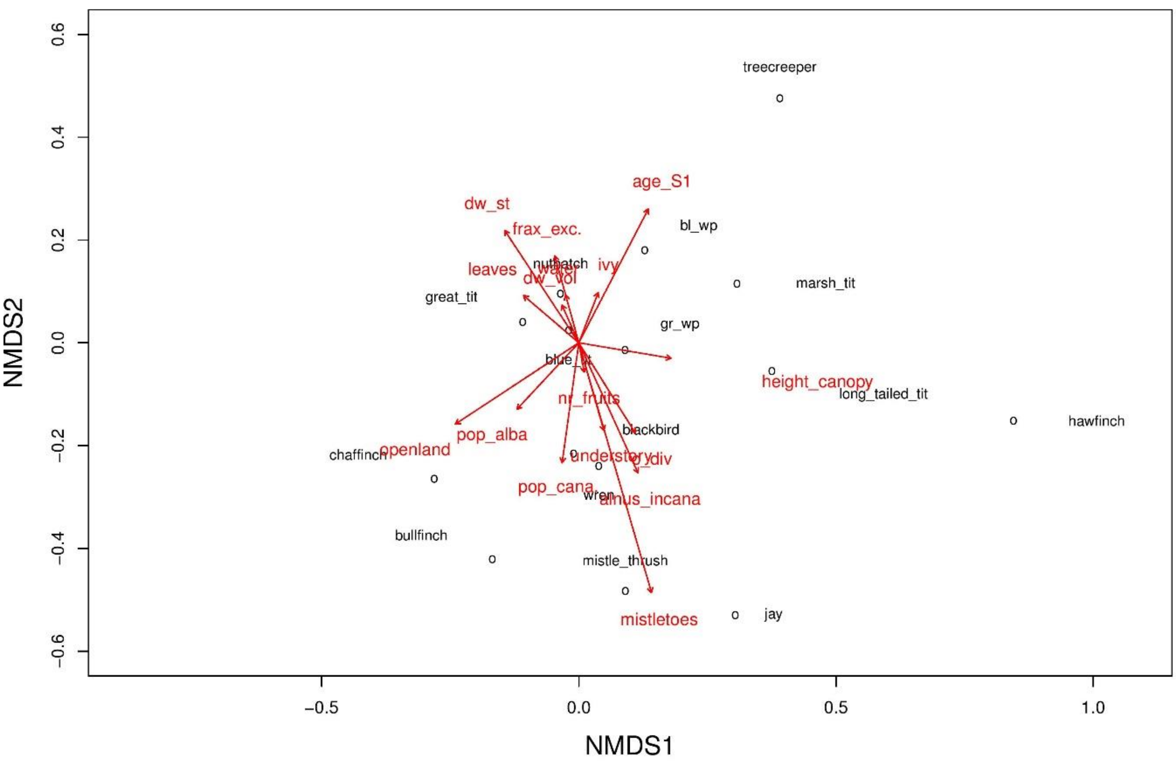


*Figure 10 NMDS plots with labelled bird species and environmental variables.*

A permutational multivariate analysis of variances using distance matrices (= Permanova) was performed to check which environmental predictors significantly affect the community composition of the 15-bird species, which were detected in at least 10 plots. With “adonis” the Permanova was performed to test the relationship between the dissimilarity matrix of the bird community and environmental predictors (method= “Bray “, permutation= 999). The order of the predictor input was chosen by the $R^2$ value (of Table 8), meaning that predictors with high $R^2$ values were put first. Mistletoes and deadwood volume have significant p- values (see Table 9), indicating that these two predictors have strong effects on community structuring, although the explained variance is very low.
Adonis confirms and NMDS shows, that the number of mistletoes is the most important predictor.

*Table 8 Results of the function "adonis", signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1*

| | Df | SumsOfSqs | MeanSqs | F.Model | R2 | Pr(>F) | |
|---|---|---|---|---|---|---|---|
| **mistletoes** | 1 | 0.3933 | 0.3933 | 6.3395 | 0.0864 | 0.001 | *** |
| **age_S1** | 1 | 0.1243 | 0.1243 | 2.0038 | 0.0273 | 0.053 | . |
| **openland** | 1 | 0.0868 | 0.0868 | 1.3986 | 0.0191 | 0.207 | |
| **alnus_incana** | 1 | 0.0726 | 0.0726 | 1.1699 | 0.0159 | 0.324 | |
| **st_dw** | 1 | 0.0746 | 0.0746 | 1.2032 | 0.0164 | 0.326 | |
| **pop_cana.** | 1 | 0.0183 | 0.0183 | 0.2949 | 0.0040 | 0.921 | |
| **c_div** | 1 | 0.0427 | 0.0427 | 0.6883 | 0.0094 | 0.705 | |
| **height_canopy** | 1 | 0.1235 | 0.1235 | 1.9914 | 0.0271 | 0.060 | . |
| **understory** | 1 | 0.0529 | 0.0529 | 0.8533 | 0.0116 | 0.548 | |
| **pop_alba** | 1 | 0.0543 | 0.0543 | 0.8755 | 0.0119 | 0.550 | |
| **frax_exc.** | 1 | 0.0834 | 0.0834 | 1.3441 | 0.0183 | 0.230 | |
| **leaves** | 1 | 0.0392 | 0.0392 | 0.6312 | 0.0086 | 0.735 | |
| **Ivy** | 1 | 0.0417 | 0.0417 | 0.6718 | 0.0092 | 0.680 | |
| **water** | 1 | 0.0163 | 0.0163 | 0.2629 | 0.0036 | 0.952 | |
| **vol_dw** | 1 | 0.1259 | 0.1259 | 2.0298 | 0.0277 | 0.050 | * |
| **nr_fruits** | 1 | 0.0410 | 0.0410 | 0.6609 | 0.0090 | 0.684 | |
| **Residuals** | 51 | 3.1637 | 0.0620 | | 0.6946 | | |
| **Total** | 67 | | | | 1.0000 | | |

# Discussion

## Bird abundances

The three most abundant bird species in our study are Great Tit, Blue Tit and Eurasian Nuthatch. These bird species are very common in Austria, they have a broad ecological amplitude and can inhabit a wide range of different habitats (Reichholf-Riem 2003a; 2003b; 2003c). In the study of Adrion (2016), the most abundant bird species was Common Chaffinch with 569 individuals (inside 403) followed by Great Tit with 480 (inside 364) and Song Thrush (inside 293). In our study, Common Chaffinch was only the 11th most abundant bird species with 43 individuals (inside 38). The change in abundance of Common Chaffinch shows clearly that this bird species is a partial migrant. Part of the population in Central Europe moves to the Mediterranean for overwintering. Schifferli (1963) states, that in Switzerland approximately only 5% of all Chaffinches are overwintering (cited from Glutz von Blotzheim & Bauer 1997a). Numbers of Great Spotted Woodpecker, a permanent resident species, are nearly the same (winter 130x, spring: 94x), in winter slightly more birds were detected.

There is a strong difference in the number of Mistle Thrushes (winter: 120x, spring: 4x). Mistle Thrushes are common breeding birds in montane and subalpine levels in Austria, but in the lowland they are uncommon breeding birds (Glutz von Blotzheim & Bauer 1988; Stadler 2003). Mistle Thrushes are partial migrants and most of the Northern European population leaves their breeding habitat in winter. In Austria, a shift in the non-breeding season from the breeding habitat to the lowlands is taking place. Interestingly, the Mistle Thrush winter distribution depends strongly on the abundance of mistletoes. Due to planting of host trees since the last two centuries the mistletoe distribution in Europe expanded and so did the breeding and winter distribution of Mistle Thrush too (Guest 2010).

## Effects of vegetation & landscape parameters on species richness and diversity

Species richness was predominantly explained by two environmental parameters. It increased with the number of mistletoes and with the proportion of alder in the canopy layer. Species diversity was also related to the abundance of mistletoes but also depended on the distance to open land. Species diversity decreased with distance to open land. 80% of the best 100 diversity models include the proportion of alder as well. No spatial autocorrelation was detected for the two best GLMs, meaning that the spatial position of the census points did not bias our results. All other independent variables (leaf litter coverage, trees overgrown by ivy, understory density, height of canopy, number of fruiting trees and shrubs, canopy diversity, age of the tree layer, deadwood volume, standing deadwood, proportion of white poplar and ash in the canopy layer) did not significantly affect species richness and diversity of floodplain forest bird assemblages.

## Grey alder (*Alnus incana*)

The proportion of grey alder in the canopy layer was a strong predictor for species richness as well as for species diversity. Grey alder is a typical softwood forest species in montane levels in Europe and in Alpine foreland. Therefore, it is resistant against summer floods. In the Viennese riparian forest, grey alder gets already rarer in abundance (Ellenberg 1996). In our study, all alder trees in the canopy layer were located south of the dam, showing clearly that grey alder needs more humid sites frequently affected by flooding events and does not prefer hardwood forest conditions. Adrion (2016) states that at alder stands the insect abundance might be higher due to soggier conditions. Another explanation for the importance of alder in winter might be that alder seeds, which usually stay in woody female catkins on the tree in winter, provide an additional food source for birds. Glutz von Blotzheim (1993a; 1997a; 1997b) lists many resident bird species feeding on alder seeds.

## Deadwood

There was no significant relationship between the amount of deadwood and species richness or species diversity, although the number of standing deadwood was included in the best richness and diversity model. Deadwood is often correlated with bird species richness because it provides habitat, feeding and overwintering sites for many insects as well as for birds (Nilsson 1979). Especially saprophytic insects benefit from a large amount of lying or standing deadwood (Müller & Bütler 2010). In our study bird richness and diversity decreased with increasing number of standing deadwood. This irritating result was found by Adrion (2016) as well. Waringer (2017) also found a negative effect of standing deadwood on Collared Flycatcher (*Ficedula albicollis*), normally a typical deadwood bird. The best explanation might be that, at the National Park Donau-Auen, the amount of deadwood is an indicator of former intense forestry management. It seems likely that deadwood indicates monotonous, unattractive plots in the floodplain forest. When the national park was established in 1996, forestry, including thinning out forest stands, was stopped. It seems likely that many young trees died off afterwards. These stands with young standing dead trees with a low trunk diameter might be worthless for birds and many insect species. Deadwood- relying insect assemblages need deadwood structures in every decomposition state and additionally depend on various other parameters like solar radiation and microclimate (Vodka et al. 2009; Bouget et al. 2013). It is possible that the deadwood inhabiting insect community of the riparian forest still does not have sufficient suitable habitats and still did not recover from the former intense forest management measures. Contradicting to the possible explanation of the lack of xylobiotic insects, Stürzenbaum (2013) found an extremely high species richness of xylobiotic beetles in the floodplain forest of the National Park Donau-Auen. But she was not able to find any influence of deadwood (degree of decay, volume of standing and lying deadwood) on xylobiotic Coleoptera on small spatial scales. This might be because in her study, lots of deadwood originates from box elder (*Acer negundo*), an introduced species not native in Austria. Many beetle species might not be able to use deadwood of this introduced tree species. Interestingly her study, as well as the study of Vodka et al. (2009) and Gossner et al. (2013), could not detect any influence of the available amount of deadwood on the species richness and abundance of saproxylic beetles. They state that other factors might be more important. Furthermore, it is already questioned in Nilsson (1979) if standing deadwood is related to density of bird food.

Distribution of deadwood on the landscape scale might be more important for the absence or presence of saproxylic organisms (Müller & Bütler 2010).

### Distance to open land

Species diversity decreased with the distance to open land. Adrion (2016) did not find a significant relationship. It seems likely, that in winter the edge effect is more important than in spring. The edge effect explains the phenomenon that boundary habitats have a greater biodiversity than the adjacent bigger ecosystems (Schaefer 2012). Many of our plots may have been affected by such edge effects because the minimum distance to open land from the point center was only 50 meters. The diversity is significantly higher in plots near open land. This could be due to edge species which are more abundant in ecotones and due to more favorable environmental conditions at the forest`s edge. Furthermore, a shift to plots near open land in winter might occur because some bird species enlarge their home range in winter and search for food not only in the forest, but also on meadows and farmland (Bezzel & Prinzinger 1990).

### Distance to permanent water bodies

Our hypothesis was that species richness and species diversity are higher at plots near permanent water bodies due to greater food supply originating from the higher number of aquatic insects. We did not find any evidence for this hypothesis. There are two possible reasons for this outcome. Due to the warm weather conditions, nearly all our "permanent" water bodies ran completely dry before our fieldwork started and therefore aquatic insects might have migrated to other water bodies for overwintering or egg laying. It is possible, that due to extraordinary weather conditions, the impact was lower than normally in winter. The other explanation could be that in winter the amount of available aquatic insects is too low to affect the occurrence of insectivorous birds. Hence, it seems likely, that in winter, aquatic insects do not play a key role in nutrition of bird species, while they represent an important food source in spring when side arms of the river Danube are still filled with water. Therefore, species richness was significantly influenced by the distance to water bodies in the study of Adrion (2016). Also Iwata et al. (2003) reported, that streams support insectivorous birds in riparian forests in spring and that aquatic insect abundance depends on stream geomorphology.

### Forest age

Many studies document a positive effect of forest age on bird species abundance and diversity. Further, more bird species are overwintering in older than in younger stands (Manuwal & Huff 1987; Donald et al. 1997; Laiolo 2002; 2003). Older forests provide more tree holes (used for breeding and roosting) and deadwood (utilized by foraging insectivorous birds). Tree volume in old forests stands increases and tree bark is more structured leading to better foraging conditions for trunk feeders (Laiolo 2002). However, neither Adrion (2016) nor this study found a significant positive effect of forest age and height of canopy on species diversity and richness. The National Park Donau-Auen was established just 20 years ago in 1996 and so all investigated forest stands are remnants of the former intense forestry management. Due to these forestry measures implemented until recently, older stands may still lack typical features of mature forests. Additionally, no significant correlation between forest age and the amount of deadwood could be detected in our study. Also Nilsson (1979) did not find a correlation between forest age and standing deadwood. He stated that deadwood must be an indicator for forest management and not for forest age. Another explanation why we could not detect any changes in bird assemblages related to forest age might be that our sites did not show big age differences. All tree layers were between 20 and 98 years old, with an average of 58 years.

### Fruiting trees and shrubs

The abundance of fruits was included in the best model testing for effects of habitat and landscape variables on bird diversity although it did not have a significant effect. Food supply proved being the most important parameter for bird assemblages in this study and therefore the parameter number of fruits should be more important. Fruit availability was also the best predictor of species richness for ground-foraging birds at the study of Carrascal et al. (2012), which was conducted in a Mediterranean oakwood forest in winter. One possible explanation that fruits did not emerge as important variable in our study may be related to our assessment of fruiting trees and shrubs. Fruiting trees and shrubs were noted only once during the visit of the census points in December. It is likely that the amount of seeds and berries declined over time (eaten up or wind dispersal) and so in February less berries and seeds remained on the plants. Hence, the December count of fruits and seeds might not have been representatively assessed the situation for the entire winter. Old man`s beard (*Clematis vitalba)* was the most abundant plant species with seeds. Only few bird species, like Bullfinch, have its seeds on its nutrition list (Glutz von Blotzheim & Bauer 1997a).

### Ivy (*Helix hedera*)

No significant relationship between species richness or species diversity and the number of trees, overgrown by ivy, was found. This might be because of the low ivy-tree abundance on our plots. Additionally, ivy berries were still not ripe in February. The ivy trees could therefore not provide food supply but only hiding spots and contribute to the structural diversity of the forest sites. It might be possible that ivy plays a bigger role in early spring when fruits are ripe. Some studies include ivy as a parameter but very often it is not considered in further analysis because of its low abundance (Laiolo et al. 2003). Müller (2005) only found two bird species which were correlated with trees overgrown by ivy.

### Leaf litter

Leaf litter coverage might only play a greater role for ground feeding birds which search for invertebrates and seeds on the ground. Therefore, it is not important enough for showing any significant effect on the whole bird community.

Pierce & King (2011) compared the avian community and habitat characteristics of floodplain forests with valley plugs and with unchannelized streams in Tennessee/ USA. They found out, that the probability of occurrence for most bird species increased with litter layer depth and density of woody stems. The Yellow-Breasted Chat (*Icteria virens*), an omnivorous bird species, even had a relationship with both- litter depth and litter coverage. At unchannelized sites, the forest showed more mature characteristics like a higher leaf litter coverage, more forb- and woody vegetation. Bird species richness was higher at unchannelized sites with these characteristics.

## Mistletoe (*Viscum album*)

In our study, the number of mistletoes was the strongest environmental parameter in shaping the bird community in the National Park Donau-Auen in winter. Bird diversity and richness increased significantly with the number of mistletoes.
Mistletoes can be seen as keystone resources in many ecosystems worldwide (Watson 2001; Napier et al. 2014). Although the size and biomass of mistletoes is small, their impact is extraordinarily big. Bennetts (1996) found out that in Colorado pine forests, dwarf mistletoe (*Arceuthobium* sp.) abundance is a highly significant predictor for bird richness. He also found a significant correlation of dwarf mistletoe infection with diversity and abundance of cavity nesting birds. Infected trees and branches are more likely to die off resulting in snags and hollow trunks.
The European mistletoe (*Viscum album*) is an evergreen, hemiparasitic plant species which is native to Europe (Nierhaus-Wunderwald & Lawrenz 1997; Briggs 2011). The mistletoe is pollinated mainly by flies but 37 insect species are recorded living on the European mistletoe. 12 insect species are living exclusively on the European mistletoe (Hellrigl 2006). Therefore, mistletoes are important habitats for arthropods in the canopy layer (Lázaro-González et al. 2017) and can be used as foraging substrate for insectivorous birds and as nesting and roosting sites (Watson 2001). Mistletoe accumulations in the canopy layer of tree hosts even enhance the structural diversity in the canopy layer and provide hiding spots during the leafless winter period due to its evergreen leaves and its dense growth form.
Its (pseudo-) fruits are white, sticky berries which ripen from November to December. The mistletoe relies on birds for dispersal, important vectors are Mistle Thrush (*Turdus viscivorus*), Fieldfare (*Turdus pilaris*), Waxwing (*Bombycilla garrulus*) and Blackcap (*Sylvia atricapilla*) (Nierhaus-Wunderwald & Lawrenz 1997; Briggs 2011). Mistletoe distribution partly corresponds with migration routes of birds but there are no strict correlations (Zuber 2004). Mistletoe berries are an important food source, some bird species even defend their mistletoe clumps. Mistle Thrushes defending mistletoes in winter even had a better breeding success in spring than the migrating birds, showing the importance and influence of mistletoes as winter food for Mistle Thrushes (Guest 2010). Food availability might be the main reason why mistletoes are a significant predictor.
In our study area, the number of mistletoes is significantly higher south of the dam, showing clearly a preference on host plants which are common softwood forest species, like poplar and willow. More hybrid poplar stands are also located south. Some of them contained a high number of mistletoes in our study. Schratt-Ehrendorfer (2011) states, that the high number of mistletoes of willow and poplar population shows the overaging of the softwood forest. Due to insufficient rejuvenation, because of the changed hydrodynamic, the softwood forest slowly disappears in the national park.

Hybrid poplar stands are remnants from former forestry. The national park management partly chops down hybrid poplar stands to get a more natural plant species assemblage in the forest. Mistletoe infected hybrid poplar stands show significantly less vitality than not infected stands in the national park (Knoll 2015). Infected stands are more likely to collapse, therefore a natural rejuvenation with autochthonous species can occur without any management (Baumgartner et al. 1999). Due to the importance of mistletoe clumps for wintering bird species it is preferable to maintain hybrid poplar stands with a high mistletoe infection rate.

### Understory

Understory structure was not important, although it is known that some bird species depend on forests with a diverse vertical stratification, including a well-developed and diversely structured understory (Laiolo 2002). It is possible that our classification of understory density into 3 categories was not accurate enough to detect an effect on floodplain forest bird assemblages.

## Species composition and habitat preferences

Species turnover, which explained 89% of the beta diversity, was mainly responsible for changes in species composition between the plots. Nestedness contributed only with 5%. This is nearly the same result as Adrion (2016) got in her study. Species turnover means, that some species get replaced by others due to environmental selection (Baselga 2010).
In addition, we found out, that bird assemblages north and south of the dam "Marchfeldschutzdamm" differed significantly from each other. Further, census points south of the dam were characterized by higher species richness than census points north of the dam. This is probably because alder only occurs south and mistletoes had higher numbers south of the dam. Mistletoe was the strongest predictor and therefore influences the bird distribution the most. Adrion (2016) did not find a significant difference in bird assemblages north and south of the dam. This demonstrates that food supply plays a key role in bird distribution and assemblages in winter. In spring, various other food sources appear to be more important.
Changes in the percentages of the four most abundant tree species in the canopy layer, did not significantly affect bird species composition. This also counted for breeding bird communities in our study area (Adrion 2016). Also Donald et al. (1997) found no significant relationship between tree species composition and the overall number of individual birds recorded. On the other hand, foraging insectivorous bird species can have strong tree species preferences (Gabbe et al. 2002).

The NMDS plots show that some of the environmental variables have a strong impact on the occurrence of some bird species. Great Tit, Blue Tit, Eurasian Nuthatch and Great Spotted Woodpecker did not show any preference and were distributed near the centre. This is an expected finding because these bird species are allrounders, widely distributed and are the four most abundant bird species in our study. Mistle Thrush was associated with the predictor mistletoe which is also common. The Eurasian Jay seems also to be associated with

the proportion of alder in the canopy layer and with the number of mistletoes as well. The Eurasian Treecreeper seems to rely on old stands. This might be because of his insectivorous life style. Insects can achieve higher abundances in old stands (Laiolo 2002).
Chaffinches were associated with distance to open land. It seems that in our study Chaffinches prefer forest sites which are not close to the forests edge. This is an unexpected finding because Chaffinches are known as farmland songbirds and are generalists which can inhabit a diverse range of different habitats and normally utilize forests edge and hedgerows as breeding habitats (Glutz von Blotzheim & Bauer 1997a). In general, Chaffinches are more associated with woodland edges than forest interiors (Mason 2001). In the study of Macleod et al. (2004), which was conducted in spring, foraging Chaffinches showed a strong preference for trees and woods but an avoidance of cropped areas. It is possible that Chaffinches in our study use open areas for foraging but prefer the interior of riparian forests as roosting sites in winter.
The permanova test confirms that mistletoe abundance is the most important variable shaping the structure of bird assemblages in floodplain forest along the Danube east of Vienna.

## Synopsis

Our study suggests that in the National Park Donau-Auen winter food availability is the strongest predictor for bird richness and bird diversity.
It seems likely that mistletoes and alder trees are very important winter food sources in the riparian forest for many resident bird species. Aquatic insects as a winter food source are most likely neglectable. Most of the mistletoes parasite hybrid poplar stands and therefore these stands are very important winter habitats for many bird species. As a conservation recommendation for the national park this study suggests maintaining the formerly planted, highly infected hybrid poplar stands because of its importance for overwintering bird assemblages. Further, species richness was higher south of the dam, indicating that softwood forests provide better overwintering conditions for more bird species than hardwood forests. Therefore, it is recommended to preserve the softwood forest with its alder stands by stopping the fast succession from softwood to hardwood forest. This could be achieved by improving the hydrological connectivity of the floodplain forest with the water level of the Danube through the reconnection of side arms with the Danube.

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# Appendix 1: Species list- total counts

*Table 9 Detected species, their total numbers of counted individuals as well as the number of individuals counted within and outside the 50 m radius and flying over the plot; additionally, the number of plots with records of the respective species are provided (only considering records of individuals inside the 50 m radius which were not flying over). Species are ranked according to their total number of counted individuals; bold species were excluded from further analysis.*

| English name | Scientific name | Sum indiv. | In 50 m radius | out of radius | flying over | Nr. plots records |
|---|---|---|---|---|---|---|
| Great Tit | *Parus major* | 568 | 506 | 62 | 0 | 69 |
| Eurasian Nuthatch | *Sitta europaea* | 377 | 303 | 74 | 0 | 69 |
| Eurasian Blue Tit | *Cyanistes caeruleus* | 325 | 320 | 5 | 0 | 67 |
| Great Spotted Woodpecker | *Dendrocopus major* | 187 | 130 | 55 | 2 | 57 |
| Mistle Thrush | *Turdus viscivorus* | 161 | 120 | 19 | 22 | 39 |
| Marsh Tit | *Parus palustris* | 129 | 124 | 3 | 2 | 50 |
| Common Blackbird | *Turdus merula* | 80 | 72 | 5 | 3 | 35 |
| Eurasian Bullfinch | *Pyrrhula pyrrhula* | 62 | 38 | 24 | 0 | 12 |
| Fieldfare | *Turdus pilaris* | 54 | 54 | 0 | 0 | 3 |
| Long-tailed Tit | *Aegithalos caudatus* | 46 | 42 | 4 | 0 | 17 |
| Common Chaffinch | *Fringilla coelebs* | 43 | 38 | 5 | 0 | 26 |
| European Green Woodpecker | *Picus viridis* | 41 | 7 | 34 | 0 | 6 |
| Black Woodpecker | *Dryocopus martius* | 37 | 10 | 27 | 0 | 10 |
| Common Buzzard | *Buteo buteo* | 34 | 7 | 23 | 4 | 6 |
| Hawfinch | *Coccothraustes coccothraustes* | 33 | 33 | 0 | 0 | 15 |
| Hooded/ Carrion Crow | *Corvus corone/cornix* | 32 | 2 | 26 | 4 | 2 |
| **Rook** | ***Corvus frugilegus*** | 30 | 0 | 28 | 2 | 0 |
| Eurasian Treecreeper | *Certhia familiaris* | 27 | 27 | 0 | 0 | 25 |
| Eurasian Jay | *Garrulus glandarius* | 26 | 12 | 14 | 0 | 12 |
| **Black-headed Gull** | ***Larus ridibundus*** | 25 | 0 | 0 | 25 | 0 |
| European Goldfinch | *Carduelis carduelis* | 24 | 12 | 1 | 11 | 9 |
| Common Starling | *Sturnus vulgaris* | 21 | 20 | 0 | 1 | 8 |
| Eurasian Wren | *Troglodytes troglodytes* | 17 | 15 | 2 | 0 | 12 |
| **Mute Swan** | ***Cygnus olor*** | 17 | 0 | 3 | 14 | 0 |
| Middle Spotted Woodpecker | *Dendrocopus medius* | 14 | 7 | 7 | 0 | 7 |
| **Eurasian Collared Dove** | ***Streptopelia decaocto*** | 12 | 0 | 0 | 12 | 0 |
| **Mallard** | ***Anas platyrhynchos*** | 11 | 0 | 11 | 0 | 0 |
| European Robin | *Erithacus rubecula* | 10 | 9 | 1 | 0 | 9 |
| European Greenfinch | *Chloris chloris* | 9 | 6 | 3 | 0 | 5 |
| Lesser Spotted Woodpecker | *Dryobates minor* | 8 | 4 | 4 | 0 | 4 |

| | | | | | | |
|---|---|---|---|---|---|---|
| **Tufted Duck** | ***Aythya fuligula*** | 8 | 0 | 8 | 0 | 0 |
| Goldcrest | *Regulus regulus* | 6 | 5 | 1 | 0 | 5 |
| Yellowhammer | *Emberiza citrinella* | 6 | 3 | 3 | 0 | 3 |
| **Great Cormorant** | ***Phalacrocorax carbo*** | 4 | 0 | 2 | 2 | 0 |
| **Great Egret** | ***Casmerodius albus*** | 4 | 0 | 2 | 2 | 0 |
| Stock Dove | *Columba oenas* | 4 | 1 | 2 | 1 | 1 |
| **Western Jackdaw** | ***Corvus monedula*** | 4 | 0 | 3 | 1 | 0 |
| **Common Merganser** | ***Mergus merganser*** | 3 | 0 | 3 | 0 | 0 |
| Eurasian Siskin | *Carduelis spinus* | 3 | 1 | 1 | 1 | 1 |
| Eurasian Sparrowhawk | *Accipiter nisus* | 2 | 1 | 1 | 0 | 1 |
| White-tailed Eagle | *Haliaeetus albicilla* | 2 | 1 | 1 | 0 | 1 |
| **Common Reed Bunting** | ***Emberiza schoeniclus*** | 1 | 1 | 0 | 0 | 1 |
| **Grey Heron** | ***Ardea cinerea*** | 1 | 0 | 0 | 1 | 0 |
| Northern Goshawk | *Accipiter gentilis* | 1 | 1 | 0 | 0 | 1 |
| **Northern Raven** | ***Corvus corax*** | 1 | 0 | 0 | 1 | 0 |
| **Red Kite** | ***Milvus milvus*** | 1 | 0 | 1 | 0 | 0 |
| Short-toed Treecreeper | *Certhia brachydactyla* | 1 | 1 | 0 | 0 | 1 |
| Tree Sparrow | *Passer montanus* | 1 | 1 | 0 | 0 | 1 |
| **Total** | **48** | **2513** | **1934** | **468** | **111** | **69** |

# Appendix 2: Species list- per plot

*Table 10 Number of observed species and bird counts per plot. Species nr. total (n=48): all observed species (inside and outside the 50 m radius, flying over birds and waterbird species included). Species nr. in 50 m (n=34): only species which were included in further analysis. Species numbers are ranked according to the nr. of observed species (n=34).*

| Point ID | Species nr. in 50 m (n=34) | Sum of indiv. in 50 m (n=34) | Species nr. total (n=48) | Sum of indiv. total (n=48) |
|---|---|---|---|---|
| 17 | 15 | 52 | 16 | 62 |
| 25 | 13 | 34 | 15 | 39 |
| 37 | 13 | 39 | 15 | 51 |
| 2 | 12 | 30 | 13 | 32 |
| 6 | 12 | 30 | 12 | 34 |
| 19 | 12 | 34 | 16 | 57 |
| 33 | 12 | 66 | 16 | 76 |
| 39 | 12 | 34 | 13 | 41 |
| 8 | 11 | 52 | 13 | 57 |
| 14 | 11 | 46 | 16 | 54 |
| 16 | 11 | 63 | 14 | 75 |
| 40 | 11 | 46 | 14 | 51 |
| 43 | 11 | 34 | 15 | 43 |
| 46 | 11 | 47 | 14 | 52 |
| 58 | 11 | 44 | 15 | 52 |
| 62 | 11 | 32 | 13 | 36 |
| 71 | 11 | 33 | 14 | 40 |
| 10 | 10 | 29 | 13 | 34 |
| 22 | 10 | 28 | 14 | 37 |
| 28 | 10 | 19 | 15 | 28 |
| 30 | 10 | 35 | 11 | 43 |
| 32 | 10 | 42 | 13 | 49 |
| 44 | 10 | 32 | 11 | 35 |
| 74 | 10 | 33 | 14 | 39 |
| 4 | 9 | 25 | 13 | 34 |
| 5 | 9 | 26 | 10 | 29 |
| 7 | 9 | 26 | 13 | 33 |
| 21 | 9 | 32 | 12 | 58 |
| 34 | 9 | 34 | 13 | 40 |
| 48 | 9 | 39 | 12 | 47 |
| 49 | 9 | 21 | 12 | 29 |
| 56 | 9 | 38 | 11 | 49 |
| 59 | 9 | 30 | 15 | 40 |
| 64 | 9 | 34 | 12 | 47 |
| 70 | 9 | 35 | 13 | 46 |
| 29 | 8 | 24 | 13 | 32 |

| | | | | |
|---|---|---|---|---|
| 35 | 8 | 18 | 12 | 29 |
| 61 | 8 | 21 | 8 | 24 |
| 66 | 8 | 26 | 10 | 32 |
| 67 | 8 | 28 | 9 | 32 |
| 1 | 7 | 12 | 12 | 29 |
| 3 | 7 | 17 | 10 | 27 |
| 12 | 7 | 23 | 7 | 24 |
| 15 | 7 | 28 | 10 | 36 |
| 20 | 7 | 21 | 16 | 37 |
| 24 | 7 | 11 | 9 | 16 |
| 26 | 7 | 16 | 7 | 19 |
| 36 | 7 | 19 | 8 | 23 |
| 38 | 7 | 20 | 11 | 28 |
| 45 | 7 | 19 | 10 | 23 |
| 51 | 7 | 24 | 10 | 30 |
| 60 | 7 | 17 | 13 | 30 |
| 63 | 7 | 25 | 10 | 37 |
| 68 | 7 | 18 | 7 | 18 |
| 13 | 6 | 35 | 11 | 57 |
| 23 | 6 | 16 | 10 | 26 |
| 27 | 6 | 21 | 9 | 27 |
| 31 | 6 | 18 | 12 | 29 |
| 47 | 6 | 25 | 9 | 34 |
| 54 | 6 | 25 | 9 | 39 |
| 57 | 6 | 15 | 10 | 37 |
| 72 | 6 | 17 | 11 | 24 |
| 11 | 5 | 19 | 7 | 23 |
| 52 | 5 | 23 | 8 | 32 |
| 53 | 5 | 14 | 5 | 17 |
| 65 | 5 | 8 | 9 | 17 |
| 73 | 5 | 10 | 8 | 20 |
| 41 | 4 | 8 | 4 | 10 |
| 50 | 4 | 18 | 6 | 26 |

# Appendix 3: Correlation chart

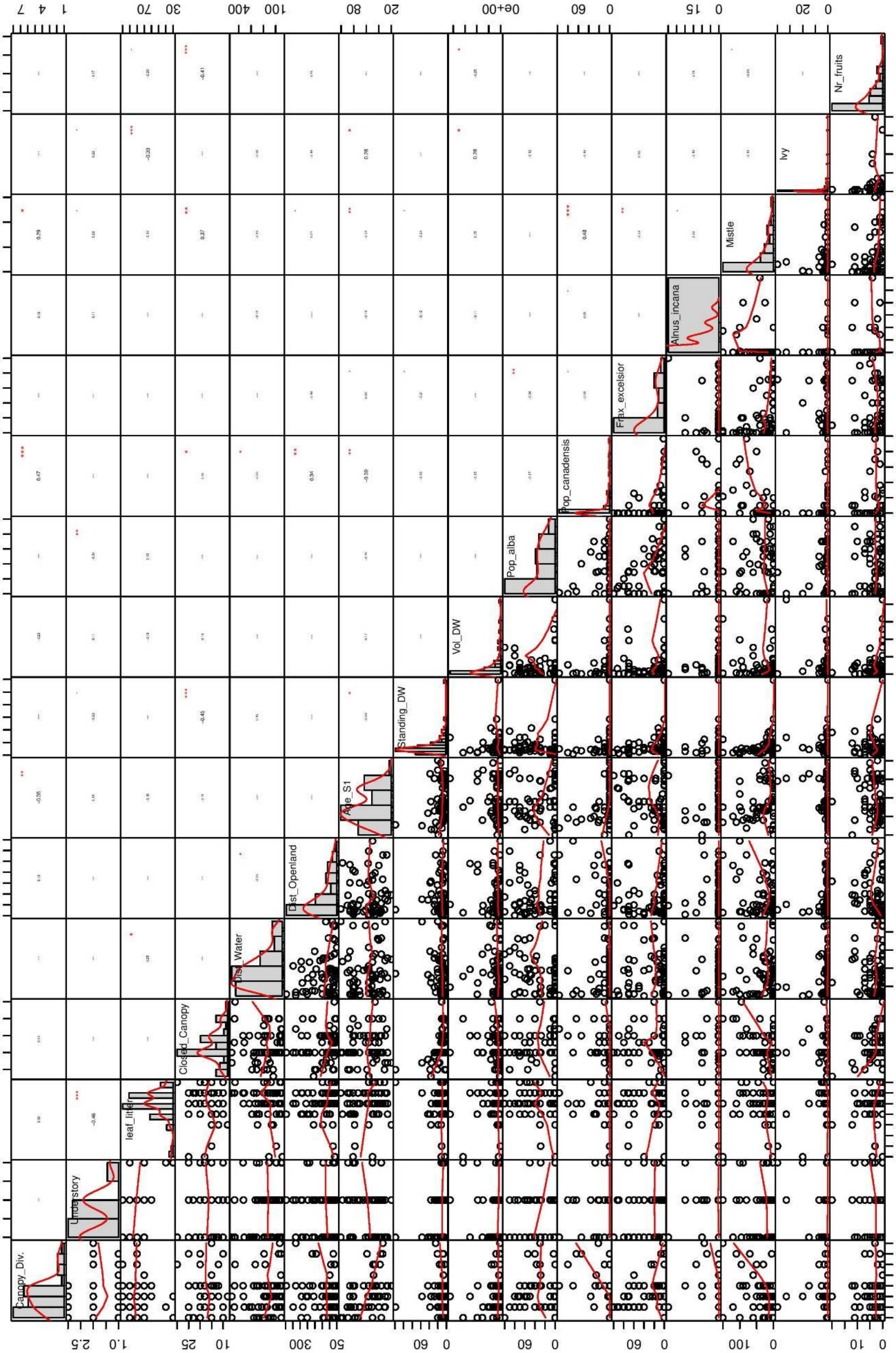


*Figure 11 Correlation chart of 16 environmental predictors assessed at 68 census points*

# Appendix 4: Glm results

*Table 11 The best 16 models for ntax. Selected automatically by "glmulti" and ranked after the AIC criterion within a range of 2 IC units.*

| Nr. | model | aicc | weights |
|---|---|---|---|
| 1 | ntax ~ 1 + st_dw + alnus_incana + mistletoes | 3.001.751 | 0.03381733 |
| 2 | ntax ~ 1 + alnus_incana + mistletoes | 3.003.717 | 0.03065162 |
| 3 | ntax ~ 1 + openland + st_dw + alnus_incana + mistletoes | 3.008.326 | 0.02434270 |
| 4 | ntax ~ 1 + water + openland + alnus_incana + mistletoes | 3.008.371 | 0.02428796 |
| 5 | ntax ~ 1 + openland + st_dw + alnus_incana + mistletoes + nr_fruits | 3.010.079 | 0.02230009 |
| 6 | ntax ~ 1 + openland + alnus_incana + mistletoes | 3.010.331 | 0.02202025 |
| 7 | ntax ~ 1 + water + alnus_incana + mistletoes | 3.011.704 | 0.02055916 |
| 8 | ntax ~ 1 + water + openalnd + st_dw + alnus_incana + mistletoes | 3.012.095 | 0.02016133 |
| 9 | ntax ~ 1 + st_dw + alnus_incana + mistletoes + nr_fruits | 3.012.206 | 0.02004975 |
| 10 | natx ~ 1 + water + openland + alnus_incana + mistletoes + nr_fruits | 3.013.319 | 0.01896440 |
| 11 | ntax ~ 1 + water + st_dw + alnus_ incana + mistletoes | 3.014.267 | 0.01808701 |
| 12 | ntax ~ 1 + openland + alnus_incana + mistletoes + nr_fruits | 3.014.487 | 0.01788915 |
| 13 | ntax ~ 1 + water + openland + st_dw + alnus_incana + mistletoes + nr_fruits | 3.014.972 | 0.01746014 |
| 14 | ntax ~ 1 + alnus_incana + mistletoes + nr_fruits | 3.015.556 | 0.01695746 |
| 15 | ntax ~ 1 + leaves + st_dw + alnus_incana + mistletoes | 3.019.236 | 0.01410750 |
| 16 | ntax ~ 1 + leaves + alnus_incana + mistletoes | 3.019.304 | 0.01405988 |

*Table 12 The best 13 models for sh_birds. Selected automactically by "glmulti" and ranked after AIC criterion within a range of 2 IC units.*

| Nr. | model | aicc | weights |
|---|---|---|---|
| 1 | sh_birds ~ 1 + openland + st_dw + alnus_incana + mistletoes + nr_fruits | -4.391.454 | 0.03768368 |
| 2 | sh_birds ~ 1 + closed_Canopy + openland + st_dw + alnus_incana + mistletoes | -4.357.380 | 0.03178058 |
| 3 | sh_birds ~ 1 + openland + st__dw + alnus_incana + mistletoes | -4.301.018 | 0.02397574 |
| 4 | sh_birds ~ 1 + openland + st_dw + pop_alba + alnus_incana + mistletoes + nr_fruits | -4.292.671 | 0.02299571 |
| 5 | sh_birds ~ 1 + openland + alnus_incana + mistletoes + nr_fruits | -4.283.703 | 0.02198745 |
| 6 | sh_birds ~ 1 + closed_Canopy + openland + st_dw + alnus_incana + mistletoes + nr_fruits | -4.283.076 | 0.02191861 |
| 7 | sh_birds ~ 1 + closed_Canopy + openland + st_dw + pop_alba + alnus_incana + mistletoes | -4.260.149 | 0.01954466 |
| 8 | sh_birds ~ 1 + openland + st_dw + mistletoes + nr_fruits | -4.258.867 | 0.01941975 |
| 9 | sh_birds ~ 1 + st_dw + alnus_incana + mistletoes | -4.238.282 | 0.01752036 |
| 10 | sh_birds ~ 1 + openland + alnus_incana + mistletoes | -4.231.670 | 0.01695066 |
| 11 | sh_birds ~ 1 + openland + st_dw + pop_alba + alnus_incana + mistletoes | -4.216.241 | 0.01569212 |
| 12 | sh_birds ~ 1 + openland + st_dw + pop_alba + mistletoes + nr_fruits | -4.200.199 | 0.01448260 |
| 13 | sh_birds ~ 1 + openland + frax_excelsior + alnus_incana + mistletoes + nr_fruits | -4.195.789 | 0.01416681 |

# Appendix 5: Understory reference pictures

*Figure 12 Reference picture for category 1 (0-25%), census point nr. 30*

*Figure 13 Reference picture for category 2 (25-50%), census point nr. 4*

*Figure 14 Reference picture for category 3 (50-100%), census point nr. 24*