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Abstract

Grassland bird species have experienced dramatic declines on a global scale due to the loss of large heterogeneous grassland patches. In our study we surveyed birds at 50 meadow sites in the eastern part of the National Park Donau-Auen (Lower Austria) from April to July 2016. In total we counted 3681 individuals and recorded 68 bird species. While species richness increased with meadow size and an increasing proportion of meadow structures, the ratio of forest edge to meadow size had a negative effect. We did not find a relationship of species richness with the degree of disturbance (distance to levee), forest edge composition (width, density, layers) and isolation of meadows from the national park border. Red-backed Shrike *Lanius collurio*, Yellowhammer *Emberiza citrinella*, and Common Buzzard *Buteo buteo* proved being indicator species for big (>5 ha) and medium-sized meadows (2-5 ha) whereas the European Bee-eater *Merops apiaster* and the Common Falcon *Falco tinnunculus* utilized exclusively big meadows. While the abundance of Yellowhammers increased with increasing meadow size, the abundance of Red-backed shrike *Lanius collurio* was positively related to the presence of hedges. Beta diversity measures indicate a high extent of nestedness in meadow bird communities, mainly shaped by varying meadow size, while species turnover generally proved being very low. Overall this study emphasize that future management strategies should target to protect large extended meadow patches and maintain or create a high diversity of meadow structures.

Keywords: meadow bird communities, nestedness, beta diversity, indicator species, grassland management, bird conservation

Zusammenfassung

Aufgrund des Verlusts von heterogenen großen Offenlandflächen ist die Zahl an Wiesen- und Offenlandvogelarten weltweit stark im Rückgang. In dieser Studie wurden Vögel auf 50 Wiesenflächen im östlichen Teil des Nationalparks Donau-Auen zwischen April und Juli 2016 untersucht. Insgesamt wurden 3681 Individuen gezählt und 68 Vogelarten nachgewiesen. Während der Artenreichtum mit der Wiesengröße und einem höheren Anteil an Wiesenstrukturen steigt, hat das Verhältnis Waldrandlänge zu Wiesengröße einen negativen Effekt. Es konnte kein Zusammenhang zwischen dem Artenreichtum der Vögel und dem Grad der anthropogenen Störung (Distanz zum Damm), der Struktur des Waldrands (Breite, Dichte, Schichten) und der Isolation der Wiesenflächen von der Nationalparkgrenze gezeigt werden. Neuntöter *Lanius collurio*, Goldammer *Emberiza citrinella* und Mäusebussard *Buteo buteo* erwiesen sich als Indikatorarten für große (>5 ha) und mittelgroße Wiesen (2-5 ha), wohingegen Bienenfresser *Merops apiaster* und Turmfalke *Falco tinnunculus* ausschließlich große Wiesen nutzten. Während die Abundanz der Goldammer positiv mit der Wiesengröße korrelierte, nahm die Abundanz des Neuntöters mit dem Vorkommen von Hecken zu. Maße zur Beta-Diversität zeigen einen hohen Grad an Nestedness in der Artenzusammensetzung von Wiesenvogelgemeinschaften, geprägt durch die unterschiedlichen Wiesengrößen, wobei der Arten-Turnover sehr gering ist. Die Studie verdeutlicht, dass zukünftige Managementstrategien des Nationalparks Donau-Auen darauf abzielen sollten, besonders große Wiesenflächen zu schützen und eine hohe Vielfalt an Wiesenstrukturen zu erhalten bzw. zu schaffen.

1. Introduction

The National Park Donau-Auen (hereafter DANP) is one of the last floodplain forests in Central Europe and was put under protection 1996 (Pfundner *et al.* 2012). Floodplain forests are complex environments representing a mosaic of heterogeneous landscapes and are characterized by unique species compositions (Tockner *et al.* 1999, Klimo & Hager 2001). They are dynamic systems shaped by seasonal changes in flooding frequency and duration (Yon & Tendron 1981). Precipitation climaxes and the snowmelt in the Alps lead to flooding events particularly between late spring and high summer (Tockner *et al.* 1999).

Floodplain forest ecosystems in Europe have undergone severe anthropogenically induced changes due to river regulation measures and termination of groundwater table, reduction of area for agricultural purposes and negative effects of intensive land use in its vicinity as well as building of hydroelectric power stations (Klimo 1998). This also counts for the DANP, where flooded areas were additionally reduced by a levee limiting inundation to a relatively small buffer zone along the Danube river.

While most of the DANP is covered by hardwood and softwood forest, also meadows embedded within this forest matrix, which are maintained by mowing, contribute substantially to its area with 705 hectares (Nationalpark Donauauen 2009). Only some of the smaller meadows were recently abandoned, which are now increasingly covered by bushes and reedbeds (Pfundner *et al.* 2012). Between 2010 and 2011, meadows of the Lower Austrian part have been evaluated in terms of their flora and vegetation status (Pfundner *et al.* 2012). Almost half of the meadow area (331 ha) received high priority status on a botanical base (Schratt 1989, Pfundner *et al.* 2012). According to this study only 8% (55 ha) of the total meadow area showed typical wetland-meadow character whereas 62% (440 ha) were considered as moderate dry meadows and 30% as dry meadows. Although these drier grassland patches are the result of the levee leading to a severe reduction of the floodplain dynamics, they are today protected according to the Flora and Fauna habitat directives of the European Union due to their specific flora and fauna (Pfundner *et al.* 2012).

A total of 101.15 km² of the DANP's floodplain area is classified as important bird area (Criteria B2, C6) (Dvorak & Berg 2009). Grasslands are an important habitat for bird species of international (FFH Bird Directive) as well as national importance (e.g. regional Red List of birds in Lower Austria; Berg & Ranner 1997). First surveys of meadow bird communities with a focus on wetland meadows (Frühauf & Wichmann 2006) and particularly considering the status of the Common Corncrake *Crex crex* (Frühauf & Sabathy 2002) were conducted in 1999.

The aim of this study is to improve the knowledge on habitat requirements of bird species in the DANP, which depend on meadows. In particular, we analysed effects of meadow size and structure as well as forest edge structure on bird species richness and composition and on the occurrence of individual species. Results of this study can be utilized to facilitate the development of an improved grassland management within the DANP.

In particular, we addressed the following research questions:

1. Which meadow characteristics do affect species richness, species abundance and species diversity of meadow-dependent birds?

Grassland birds have experienced extensive population declines because of the loss of large grassland patches (Herkert 1994, Vickery *et al.* 1994). Synchronization of mowing times, homogeneity of meadow areas and monotony of structural composition and diversity have been considered as main limiting factors for meadow-dependent (either using them as food or breeding site) bird species in the DANP (Frühauf & Wichmann 2006). Higher structural diversity on meadows is reported to support higher species richness and species diversity (Nikolov 2010). We therefore expect that the proportion of structural elements such as bushes, hedges and single trees on meadows influence species richness and species diversity. Furthermore, larger meadows are known to host more species than smaller patches (Helzer & Jelinski 1999, Usher & Erz 1994). Hence, we expect that the species-area relationship contributes significantly in explaining differences in species richness of meadow bird assemblages in the DANP. Moreover, the ratio of forest edge length to meadow size, which reflects shape of the site is expected to affect species richness and abundance of meadow depending birds.

2. To what extent do species composition and the occurrence of certain meadow-affiliated species depend on variables such as meadow size, inundation regime and specific vegetation structures? Are there indicator species for certain meadow types?

The composition of bird assemblages can be strongly affected by flooding (Ausden *et al.* 2001, Paillisson *et al.* 2002). Hence, we expect that also the structure of bird assemblages depending on meadows in the DANP is shaped by inundation regime. In particular, we evaluate if certain birds represent indicator species (e.g. de Cáceres & Legendre 2009) for the flooding regime (inundated vs. non-inundated meadows). Moreover, as the DANP is embedded in an agricultural landscape dominated by annual cultures we assume that the distance of meadows to the National Park border will shape bird communities.

3. How do nestedness and species turnover contribute to the beta diversity of meadow bird assemblages?

Beta diversity is the spatial variation of communities among sites (Whittaker 1960). Community dissimilarities have been used to analyze, how the two components species turnover and

nestedness contribute to patterns of beta diversity (Baselga 2010, Legendre 2013). Communities are nested if species-poor sites are subsets of species-rich sites (Patterson & Atmar 1986), hence reflect the species loss along environmental gradients by filtering. Calculating nestedness is a major tool to identify environmental gradients (Ulrich *et al.* 2009) as well as species dispersal and spatial connectivity between sites (Tonkin 2015). Species turnover is defined here as species replacement (Baselga 2010). According to Baselga (2010) turnover and nestedness are two antithetic processes but it is not clear yet whether metacommunities can be organized from turnover to nestedness (Ulrich *et al.* 2017). Here we define a metacommunity as a set of local patches that are connected by dispersal. We here study whether sites are nested according to their size, proportion of meadow structures and forest edge length. In contradiction, species turnover may contribute substantially to explaining changes in community composition between flooded and non-flooded meadows. A trail network extending from the levee into the woods and meadows represents a main source of anthropogenic disturbance. We therefore assume that distance to the levee influences bird communities on meadow sites.

2. Methods and Material

2.1 Study area

The DNAP extends over 43 kilometres from the region of the Oberen Lobau, Vienna to the Austrian-Slovakian border. Our study area extends about 20 km² between the villages Orth an der Donau (48°9' N, 16°42' O) and Hainburg (48°9' N, 16°57' O). Bird communities were observed from April to July 2016 on a total of 50 selected meadow areas. Only meadows within the borders of the Lower Austrian part of the National Park Donau-Auen and in the north of the Danube riverbank were selected. In the study area the DNAP is separated by a levee in a northern and a southern part since more than 100 years. A total of 25 meadows were located north of the levee and 25 south of the levee (Figure 1). The two sides are influenced by distinct inundation regimes and developed different grassland types. Flooded meadows can be found on the southern side of the levee and are characterized by almost annual inundation and higher soil fertility. Meadows north of the levee are protected against flooding events. As the summer flood in 2016 was very weak, the inundation did not disrupt the sampling efforts at all (DoRIS 2016).

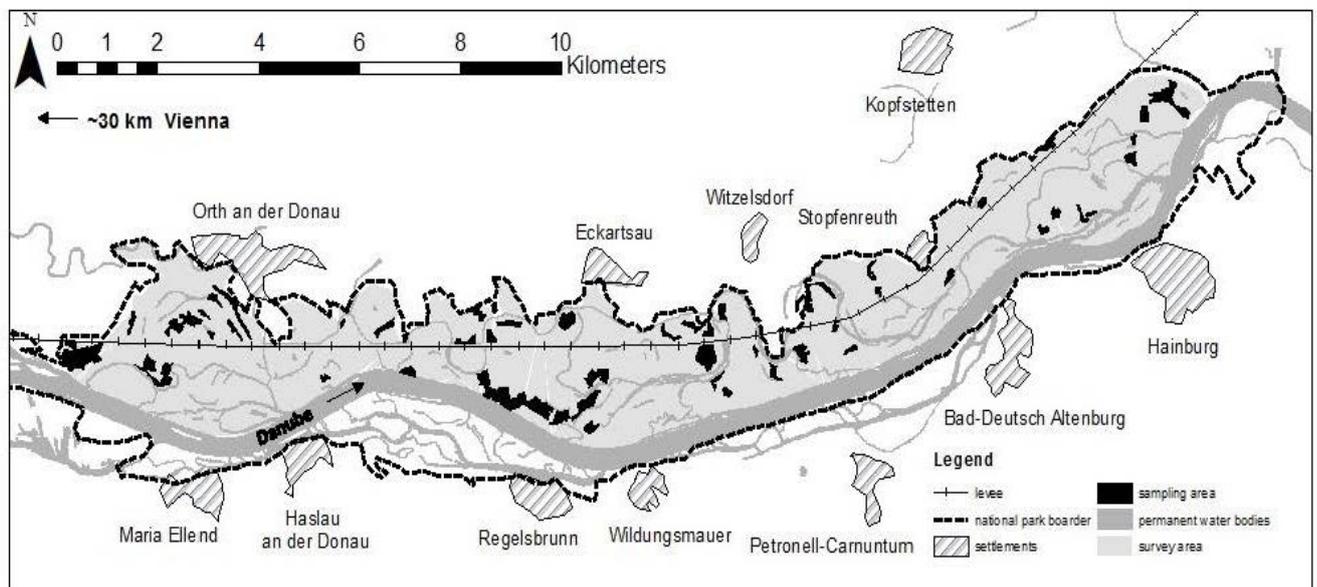


Figure 1. Map of the study area indicating the sampled meadows (black). Shape files of waterbodies and meadows were provided by ÖBf and National Park Donau-Auen GmbH.

2.2 Study sites

The selection of meadows followed a stratified random sampling. Therefore, all meadows, which have been registered for evaluating meadow management measures in 2010-2012 by Naturschutzbund NÖ, were assigned to five size categories (see Table 1). Subsequently, five

meadows of each of these categories were selected randomly for the area north and south of the levee, respectively

Table 1: Number of meadows of different size categories sampled north and south of the levee. Further the total meadow area sampled is provided for all meadow types

Size category	Number of meadows		Total meadow area (ha)	
	north of levee	south of levee	north of levee	south of levee
1 (0.5-1 ha)	5	5	3.82	3.07
2 (1-2 ha)	5	5	7.08	7.3
3 (2-3 ha)	5	5	14.78	10.3
4 (3-5 ha)	5	5	17.89	26.88
5 (5-13 ha)	5	5	28.93	38.03
Total number of meadows / Total area (ha)	25	25	72.5	85.5

All selected meadows have predominately openland character and are clearly separated from other meadows by surrounding floodplain forest. The areas of the selected meadows have been calculated using ArcMap Vers. 10.4. Shape files and further information on the meadows were provided by the National Park Donau-Auen GmbH and Österreichische Bundesforste (ÖBf).

Table 2: List of the 50 sampled meadow sites, providing coordinates, meadow size and number of bird species.

Site ID	Meadow name	Coordinates	Meadow area (ha)	Total species observed
N01	Jankwiese	48.13836, 16.66966	1.58	19
N02	Heustadlwiese	48.13878, 16.68664	12.665	34
N03	3. Grund	48.13948, 16.68853	0.728	16
N04	Westtalerin	48.13703, 16.6894	0.904	22
N05	2. Grund	48.14212, 16.69063	1.38	16
N06	2. Grund	48.13812, 16.69522	1.084	20
N07	1. Grund	48.14377, 16.69193	3	23
N08	1. Grund	48.1407, 16.69724	2.42	23
N09	Petruschkawiese	48.13776, 16.72586	0.693	17
N10	Stockmais	48.13711, 16.73758	3.15	18
N11	Weihnachtsbaum	48.13413, 16.7602	4.54	20
N12	Scheibenboden	48.13831, 16.76281	3.34	25
N13	Kl. Jungfrauenwiese	48.1355, 16.76522	2.35	22
N14	Rauhenmais	48.13742, 16.77157	2.99	18
N15	Hansleinzäunung	48.13768, 16.78534	6.06	16
N16	Cotekboden	48.13607, 16.81165	1.26	16
N17	Unknown	48.13708, 16.81886	2.22	17
N18	Schreiberwiese	48.13564, 16.82375	6.61	22

N19	Dachsenboden	48.1403, 16.85019	5.13	18
N20	Stadtblöße	48.13859, 16.82706	1.36	17
N21	Fahrtwegblöße	48.14263, 16.85502	2.27	19
N22	Hochwiese	48.14467, 16.8671	2.53	19
N23	Brückelboden	48.14229, 16.86892	0.6	12
N24	Valochacker	48.15584, 16.89686	1.5	17
N25	Deputatwiese	48.16499, 16.91431	3.64	28
S01	Forstmeisterwiese	48.13138, 16.67501	4.29	17
S02	Neubruch	48.13026, 16.67883	5.32	22
S03	Biberhäufelwiese	48.13297, 16.83629	0.579	14
S04	Nußbaumwiese	48.12757, 16.82496	1.27	14
S05	Unknown	48.12764, 16.6994	0.888	16
S06	Eschenboden	48.1298, 16.74352	3.1	22
S07	Eschenboden	48.12887, 16.76378	4.06	25
S09	Unknown	48.12926, 16.795	5.87	21
S10	Wildpretwiese	48.12244, 16.78359	4.36	22
S11	Altauwiese	48.12553, 16.79157	6.84	20
S12	Unknown	48.12106, 16.79191	2.72	21
S13	Schreiber Wasserseite	48.13258, 16.8229	8.9	18
S14	Äußerer Sand	48.12997, 16.84071	2.6	16
S15	Tiergartlwiese	48.13297, 16.848	4.46	22
S16	Materialgrube	48.13644, 16.85761	0.853	15
S17	Kanzelwiese	48.12645, 16.82873	2.07	16
S18	Zerrauwiese	48.14445, 16.88789	1.75	21
S19	Rampaldwiese	48.13317, 16.86225	1.49	14
S20	Pudelhirsch	48.15171, 16.91246	1.04	21
S21	Riesenhirsch 1-2	48.15402, 16.92188	2.91	22
S22	Herrgottshaufen	48.154, 16.91637	1.75	22
S23	Brandwiese	48.1625, 16.93636	3.32	17
S24	Neuwiese	48.1696, 16.93716	0.936	16
S25	Stadlwiese	48.1696, 16.93997	3.21	22
S26	Jägerwiese	48.1715, 16.9416	11.1	31

2.3 Bird survey

Bird surveys were conducted between 19 April and 17 June 2016. Each meadow was visited three times, once during each of the following periods: 19 April–1 May 2016, 21 May–2 June 2016, 9–17 June 2016. Surveys were exclusively conducted during good weather conditions as precipitation and strong wind is decreasing bird activity (Bruni *et al.* 2014). Further, all bird counts were only made from sunrise until 4 hours after dusk to cover the time period of maximum bird activity. Due to its high conservation value, in case of the Corncrake (*Crex crex*) also random observations were noted.

To assess a meadow's bird assemblage, the entire meadow area was surveyed by walking along forest edges and crossing the central part of the meadow for a standardized time accounting for differences in meadow size (compare Table 3). All birds encountered visually or acoustically were recorded not considering birds without clear affiliation with the surveyed meadow (e.g. overflying birds). Overflying birds and raptors were only registered if they showed clear hunting activities or foraging behaviour. We also noted if birds were recorded at the forest margin or if they used meadow structures. For birds observed on meadows, it was further noted which vegetation structure they used: trees, scrubs, hedges, reeds or tall forbs. Finally we treated all observed species and a subset of birds which are affiliated to meadows and forest margins (either using them as food source or either using them as breeding habitat according to Glutz von Blotzheim & Bauer, 1985, 1988, 1989, 1993, 1994) separately in subsequent analyses (see Table 4).

Table 3: Standardized observation time for meadows of different size classes

Area (ha)	Time (min)
0.5-1	10
2-4	20
5-8	30
9-16	40

2.4 Habitat variables

Structural complexity of the forest margin was quantified by estimating width of the forest edges in meters (m) and vertical density of forest margin in percentage (%) hereinafter referred as forest edge density. Forest edge density was conducted by entering the forest margin and estimating light transmission into the margin. This was done four times for each meadow for each direction (N, S, E, W) (see Appendix 2). Furthermore length of forest margins were calculated in meters (m) using Google measurement tool. The ratio of forest edge length to meadow size was calculated as this measure reflects shape of the meadows. Small ratio indicates more circular shape and bigger ratio more complex shape of the meadows (Spanhove et al. 2009, Temple 1986)

Additionally structural habitat elements per meadow sites were first marked in a field map using satellite pictures of 2016 provided by Googlemaps. We distinguished between bushes, single trees, hedges, reeds and tall forbes (see Appendix 2). Hereinafter these structures are also merged as meadow structures. Coverage in percentage (%) of these structures was later on calculated using Google-maps measurement tools.

3. Statistical analysis

For all analyses a significance threshold of $p \leq 0.05$ was determined. All variables were tested for normal distribution and were transformed as following: meadow area was $\log(x+1)$ transformed and length of forest margins in meters and the ratio forest margin length to meadow size data were log transformed.

3.1 Species richness

Species richness analysis have been calculated both with total number of all observed birds hereinafter referred as total birds and meadow-affiliated birds (see Table 4).

To evaluate which habitat variables affected species richness of all birds linear regressions models and generalized linear models (GLM) have been calculated with Statistica 64 (2014). GLMs have been calculated with predictor values, which have shown significant correlation to species richness or species diversity in linear regression models before. As the predictor values meadow size and ratio forest edge were significantly correlated they have been treated separately in two GLMs. Residuals of linear regression with meadow size were used to test for differences between northern and southern sites using T-test's.

3.2 Indicator species

In order to determine indicator species for flooded and non-flooded meadows as well as meadow size classes (see below), the software package Indicspecies (e.g. de Cáceres & Legendre 2009) and R-Core project (2015) was used. We used the IndVal-method (Legendre 2009, Legendre *et al.* 1997) as it suits best for analyses of species-habitat associations (de Cáceres & Legendre 2009). We used the multipatt-function once only using abundances of meadow birds and once considering the abundance data of all bird species. For detecting indicator species for a certain meadow size we grouped meadows into small (0.5-2.5 ha), medium (2.5-5 ha) and large meadows (>5 ha). Calculations were again performed using the multipatt-function.

Overlap of species

3.3 Overlap of species assemblages between meadow types

To analyse the overlap of species assemblages recorded on meadows north and south of the levee the online version of Venny 2.1 was used.

3.4 Nestedness

The program BINMATNEST was used to test for nestedness of recorded species assemblages using 500 iterations (Rodríguez-Gironés & Santamaría, 2006). The rank of meadows calculated by BINMATNEST was then related to the habitat variables meadow size, forest edge length, forest edge density and meadow structures using Spearman rank correlations calculated in Statistica 64 (Statsoft 2014). P values were FDR corrected to account for multiple testing (Yoav *et al.* 1995).

3.5 Beta diversity

Overall Beta diversity of meadow bird assemblages β_{SOR} was calculated and partitioned into nestedness β_{SNE} and species turnover β_{SIM} components (Baselga 2010) using R Studio (R Development Core Team, 2006) and the package Betapart (Baselga 2010). A β ratio ($\beta_{\text{SNE}}/\beta_{\text{SOR}}$) <0.5 indicates that beta diversity is determined predominantly by species turnover, a β ratio >0.5 highlights nestedness as the dominant component (Dobrovolski *et al.* 2012).

Additionally, we used multiple site dissimilarities indices proposed by Ricotta and Pavoine (2015) because these measures also include information about absences and are not only based on pairwise dissimilarities which could be inappropriate if sites are viewed as a collection of potentially interacting units (Ricotta & Pavoine 2015). Therefore, we used the R package npGSEA (Larson *et al.* 2014).

We calculated β^x ; a measure that reflects site similarity (number of species presences). Its dissimilarity counterpart is β^+ . β^+ is the number of absences of species, which measures multiple site dissimilarity as total number of absences in the matrix, β_T ; measured by the unexpected species absences that deviate from a perfectly nested pattern and β_N ; number of absences of species that conform to a perfectly nested pattern (Ricotta *et al.* 2015).

3.6 Pairwise-site dissimilarities

Pairwise dissimilarities were measured with package Betapart (Baselga, 2010). This method partitions the pairwise Sørensen dissimilarity into species spatial turnover and nestedness resultant dissimilarities. Then multiple regression models were calculated with Euclidian distances of habitat variables and dissimilarity matrices once for meadow-affiliated birds and once for the total bird species assemblage. The aim was to test if certain habitat variables do have a significant relationship with beta diversity (Xinfeng *et al.* 2015). Because autocorrelation may affect the analyses we worked with partial Mantel tests provided by the Vegan package (Oksanen *et al.* 2007) in R Studio.

4. Results

A total number of 3681 individuals and 68 species were recorded during the three survey rounds (Appendix 1) of which 20 species are of European and/or global conservation concern (SPEC1-3). Nine species are birds of the bird directive Appendix 1 (see Table 4).

A total of 49 species and 2469 individuals were considered as meadow-affiliated birds as (see Table 4). Taxonomy follows Svensson *et al.* 2011. In the north of the levee 42 species and 1331 individuals of meadow-affiliated birds were recorded whereas in the south 36 species and 1138 individuals were recorded. Species richness ranged from 12 to 34 species per meadow. Mean species richness (\pm SD) of all birds of northern sites is 19.76 (\pm 4.53) and of southern sites 19.48 (\pm 4.03). Mean species richness of meadow-affiliated birds are very similar on both sites: for northern sites 11.36 (\pm 3.39) and for southern sites 11.12 (\pm 2.42). Mean abundance of all birds for northern sites is slightly higher (mean = 54.32) than for southern sites (mean = 45.52). Furthermore abundance of all birds correlates significantly with species richness ($r = 0.739$, $p < 0.0001$)

Table 4: Species (in alphabetic order) recorded at meadows north and south of the levee, their abundance and conservation status. Species in bold are meadow- affiliated birds.

Scientific species name	English name	Counted birds		Conservation status*
		North	South	
<i>Accipiter gentilis</i>	Northern Goshawk	2	2	
Accipiter nisus	Eurasian Sparrowhawk	3	3	
Acrocephalus arundinaceus	Great Reed Warbler	1	0	
Acrocephalus palustris	Marsh Warbler	3	12	
Aegithalos caudatus	Long-tailed Tit	74	89	
Anthus trivialis	Tree Pipit	11	0	
<i>Aquila heliaca</i>	Eastern Imperial Eagle	0	2	SPEC1, A1
<i>Ardea cinerea</i>	Grey Heron	2	0	
Buteo buteo	Common Buzzard	17	13	
Carduelis carduelis	European Goldfinch	55	54	
<i>Certhia familiaris</i>	Eurasian Treecreeper	5	8	
Chloris chloris	European Greenfinch	9	9	
Ciconia nigra	Black Stork	2	0	SPEC3, A1
<i>Coccothraustes coccothraustes</i>	Hawfinch	52	51	
Columba oenas	Stock Dove	1	4	
Columba palumbus	Common Wood Pigeon	33	14	
<i>Corvus corone</i>	Carrion Crow	20	7	
<i>Corvus monedula</i>	Western Jackdaw	0	2	
Coturnix coturnix	Common Quail	1	0	
Crex crex	Corncrake	0	2	
<i>Cuculus canorus</i>	Common Cuckoo	1	5	
<i>Cyanistes caeruleus</i>	Blue Tit	122	86	
<i>Dendrocopos major</i>	Great-spotted Woodpecker	64	35	
Dryobates minor	Lesser-spotted Woodpecker	6	2	
<i>Dryocopus martius</i>	Black Woodpecker	9	2	A1
Emberiza citrinella	Yellowhammer	138	80	
<i>Erithacus rubecula</i>	European Robin	6	3	
Falco subbuteo	Eurasian Hobby	4	1	
Falco tinnunculus	Common Krestel	4	9	SPEC 3
Ficedula albicollis	Collared Flycatcher	32	76	A1

<i>Ficedula hypoleuca</i>	European Pied Flycatcher	3	2	
<i>Fringilla coelebs</i>	Common Chaffinch	26	49	
<i>Garrulus glandarius</i>	Eurasian Jay	21	10	
<i>Hippolais icterina</i>	Icterine Warbler	9	22	
<i>Hirundo rustica</i>	Barn Swallow	29	10	SPEC 3
<i>Jynx torquilla</i>	Eurasian Wryneck	1	0	SPEC 3
<i>Lanius collurio</i>	Red-backed Shrike	12	9	SPEC3, A1
<i>Leiopicus medius</i>	Middle Spotted Woodpecker	15	16	A1
<i>Locustella luscinioides</i>	Savi's Warbler	0	1	
<i>Merops apiaster</i>	European Bee-eater	26	3	SPEC3
<i>Milvus migrans</i>	Black Kite	0	5	SPEC 3,A1
<i>Muscicapa striata</i>	Spotted Flycatcher	21	12	SPEC3
<i>Oriolus oriolus</i>	Eurasian Golden Oriole	1	4	
<i>Parus major</i>	Great Tit	229	208	
<i>Passer montanus</i>	Eurasian Tree Sparrow	1	0	SPEC3
<i>Pernis apivorus</i>	European Honey Buzzard	5	6	A1
<i>Phasianus colchicus</i>	Common Pheasant	7	0	
<i>Phoenicurus ochruros</i>	Black Redstart	1	0	
<i>Phoenicurus phoenicurus</i>	Common Redstart	2	0	SPEC2
<i>Phylloscopus collybita</i>	Common Chiffchaff	32	33	
<i>Phylloscopus sibilatrix</i>	Wood Warbler	0	3	SPEC2
<i>Phylloscopus trochilus</i>	Willow Warbler	1	0	
<i>Picus viridis</i>	European Green Woodpecker	8	4	SPEC 2
<i>Poecile palustris</i>	Marsh Tit	20	18	SPEC3
<i>Prunella modularis</i>	Dunnock	0	3	
<i>Regulus ignicapilla</i>	Common Firecrest	0	2	
<i>Milvus milvus</i>	Red Kite	0	1	SPEC 2, A1
<i>Serinus serinus</i>	European Serin	0	1	
<i>Sitta europaea</i>	Eurasian Nuthatch	47	40	
<i>Streptopelia turtur</i>	European Turtle Dove	14	8	SPEC 3
<i>Sturnus vulgaris</i>	Common Starling	350	224	SPEC3
<i>Sylvia atricapilla</i>	Eurasian Blackcap	333	356	
<i>Sylvia communis</i>	Common Whitethroat	1	1	
<i>Sylvia curruca</i>	Lesser Whitethroat	3	1	
<i>Troglodytes troglodytes</i>	Eurasian Wren	0	4	
<i>Turdus merula</i>	Common Blackbird	35	31	

<i>Turdus philomelos</i>	Song Thrush	46	43	
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*conservation status: SPEC = Species of European Conservation Concern; SPEC1 = species of global conservation concern or European conservation concern; SPEC2 = species with unfavourable conservation status whose population is concentrated in Europe, SPEC3 = conservation status is unfavourable but population is not concentrated in Europe; A1 = species listed in bird directive annex 1, which are vulnerable and in danger of extinction.

4.1 Species richness

Univariate linear regressions show that richness of all observed species and meadow-affiliated birds significantly increased with meadow area (Fig 2a, d) and length of forest edge (Fig. 2b, f). Species richness of meadow-affiliated birds also decreased with the ratio forest edge length to meadow size (Fig. 2e), hedges positively influenced species richness of meadow-affiliated birds (Fig. 2g) as well as of all birds (2c). Isolation and distance to levee and meadow structures such as single trees, bushes and width of forest edge were not significantly related to species richness.

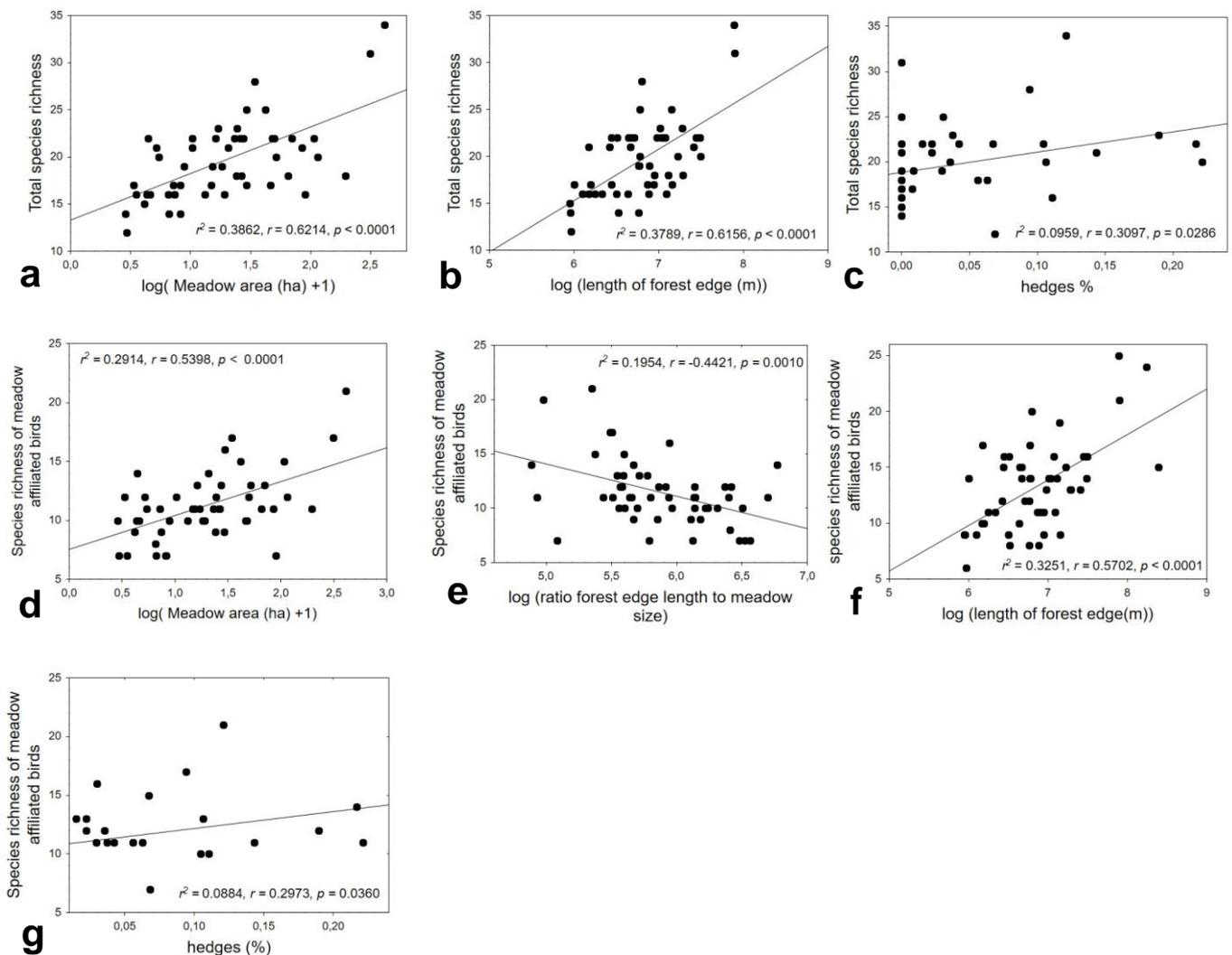


Figure 2: Simple linear regression models showing relationships between species richness of total birds and (a) meadow area, (b) length of forest margin and (c) hedges and relationships between species richness of meadow-affiliated birds and (d) meadow area, (e) ratio forest edge to meadow size, (f) length of forest edge and (g) hedges. r^2 = determination coefficient, r = correlation coefficient, p = significance value.

Species richness ($r = 0.362$, $p = 0.0098$) and abundance ($r = 0.450$, $p = 0.001$) of raptors increased with meadow size.

T-test's calculated with residuals of linear regression of species richness and meadow size didn't show significant patterns whether considering all birds ($df=0.48$, $p = 0.380$, $t = 0.885$) nor meadow birds ($df=48$, $p = 0.412$, $t = 0.828$). However variability of residuals of meadow affiliated birds of northern sites is higher than of southern sites (see Fig. 3)

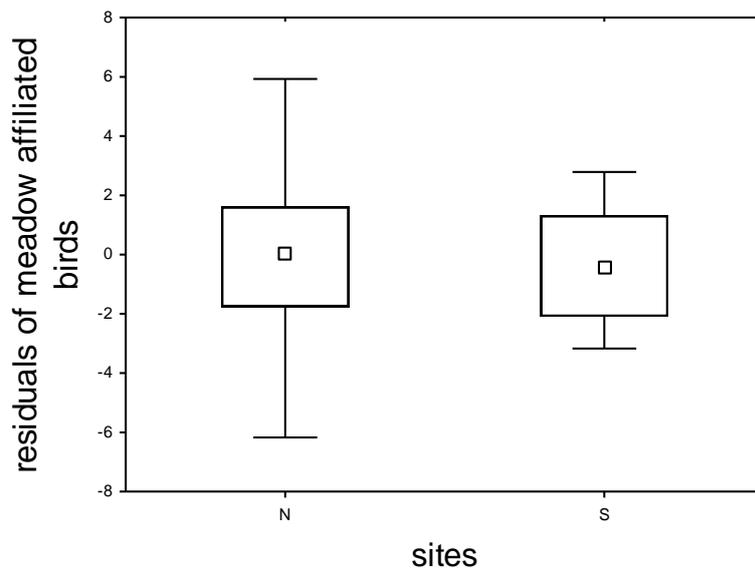


Figure 3: Means \pm SD (box) and 95% CIs (whiskers) of residuals of linear regression of species richness of meadow-affiliated birds vs. meadow size shown for meadows located north and south of the levee.

GLMs were calculated to evaluate effects of meadow variables on species richness of all birds (Table 5) and species richness of meadow-affiliated birds (Table 6.). As meadow area and the ratio forest length to meadow size were highly correlated, in both cases two GLMs were calculated including – beside additional meadow features – only meadow area (Model 1) and the ratio forest length to meadow size (Model 2), respectively. The predictor variable meadow area had a significant positive effect on total species richness (Table 5) and richness of meadow affiliated birds (Table 6). Meadow structures also had a weak positive effect on total bird species richness (Table 5). An effect of the density of forest edge on species richness was not indicated by any GLM.

Table 5: Statistical parameters of the GLMs evaluating effects of meadow parameters on the total species richness. Beside average density of forest edge and meadow structure either meadow area (Model 1) or the ratio forest edge to meadow size (Model 2) were included as explanatory variables.

Model type	df	SS	MQ	F	P	B	-95% CL	+95% CL
Model 1. $r_{\text{mult}} = 0.73$. $r^2 = 0.54$, $F = 18.69$, $p < 0.0001$								
Intercept	1	63.55	63.55	6.40	0.0148			
log (meadow area (ha) +1)	1	520.88	520.88	52.42	< 0.0001	0.74	0.54	0.95
average density of forest edge	1	32.92	32.92	3.31	0.0750	0.19	-0.02	0.39
meadow structure (%)	1	43.30	43.30	4.36	0.0422	0.20	0.01	0.40
Error	48	476.95	9.94					
Model 2. $r_{\text{mult}} = 0.54$, $r^2 = 0.29$, $F = 6.51$, $p = 0.0008$								
Intercept	1	664.71	664.71	43.41	<0.0001	-	32.67	61.36
log (ratio forest edge length to meadow size)	1	262.88	262.88	17.17	<0.0001	-0.54	-7.94	-2.75
average density of forest edge	1	20.46	20.46	1.34	0.2534	0.15	-4.79	17.74
meadow structure (%)	1	58.20	58.20	3.80	0.0571	0.24	-0.24	15.79
Error	48	734.94	15.31					

Table 6: Statistical parameters of the GLMs evaluating effects of meadow parameters on the species richness of meadow-affiliated birds. Beside average density of forest edge and meadow structure either meadow area (Model 1) or the ratio forest edge to meadow size (Model 2) were included as explanatory variables.

Model type	df	SS	MQ	F	P	β	-95 CL	+95C L
Model 1. $r_{\text{mult}} = 0.64$, $r^2 = 0.40$, $F = 10.84$, $p < 0.0001$								
Intercept	1	32.44	32.44	5.45	0.0238		0.74	9.91
log (meadow area (ha) +1)	1	178.85	178.85	30.07	<0.0001	0.64	2.09	4.50
average density of forest edge	1	3.69	3.69	0.62	0.4349	0.09	-4.20	9.62
meadow structure (%)	1	12.25	12.25	2.06	0.1578	0.16	-1.42	8.52
Error	48	285.53	5.95					
Model 2. $r_{\text{mult}} = 0.48$. $r^2 = 0.19$, $F = 4.89$, $p = 0.005$								
Intercept	1	255.15	255.15	33.38	0.0000		18.99	39.27
log (ratio forest edge length to meadow size)	1	97.51	97.51	12.76	0.0008	-0.48	-5.09	-1.42
average density of forest edge	1	1.85	1.85	0.24	0.6252	0.07	-6.01	9.91
meadow structure (%)	1	17.29	17.29	2.26	0.1392	0.19	-1.43	9.90
Error	48	366.87	7.64					

4.2 Indicator species

All calculations for identifying indicator species have been made once including all bird species and once only considering meadow-affiliated birds. Detected indicator species were the same, independently if only meadow birds or all birds were considered. Common Pheasant (considering all birds: $stat = 0.490$, $p = 0.021$; considering only meadow-affiliated birds: $stat = 0.490$, $p = 0.020$) and Lesser Spotted Woodpecker (all birds: $stat = 0.447$, $p = 0.039$; only meadow-affiliated birds: $stat = 0.447$, $p = 0.046$) are indicator species for meadows north of the levee. No indicator species were identified for meadows south of the levee. Moreover, the following indicator species were found for big meadows (5-12 ha): Red-backed Shrike (all birds: $stat = 0.575$, $p = 0.030$; only meadow-affiliated birds: $stat = 0.465$, $p = 0.013$), Common Falcon (all birds: $stat = 0.570$, $p = 0.013$; only meadow-affiliated birds: $stat = 0.570$, $p = 0.012$) and European Bee-eater (all birds: $stat = 0.465$, $p = 0.025$; only meadow-affiliated birds: $stat = 0.465$, $p = 0.013$). The Yellowhammer (all birds: $stat = 0.886$, $p = 0.001$; only meadow-affiliated birds: $stat = 0.886$, $p = 0.001$) and the Common Buzzard (all birds: $stat = 0.659$, $p = 0.31$; only meadow-affiliated birds: $stat = 0.659$, $p = 0.310$) represent indicator species for big as well as medium-sized meadows.

Spearman rank correlations show that the abundance of the Yellowhammer rose significantly with meadow size ($r = 0.627$, $p < 0.0001$) and negatively correlates with ratio forest edge to meadow size ($r = -0.486$, $p < 0.0001$). The abundance of the Red-backed Shrike was positively related to hedges ($r = 0.340$, $p = 0.016$) and meadow size ($r = 0.293$, $p = 0.039$). Common Buzzard abundance also was positively correlated with meadow size ($r = 0.400$, $p = 0.004$) and the abundance of Eurasian Blackcap was positively related to hedges ($r = 0.552$, $p < 0.0001$).

4.3 Overlap of species assemblages between meadow types

A total of 29 species occurred on meadows south and north of the levee, while 13 and seven species were recorded exclusively north and south of the levee, respectively (Table 7). However, only four species exclusively found on non-flooded northern meadows and none of the species found on regularly flooded southern meadows were recorded with more than five individuals (compare Table 4). More species have been observed on medium sized meadows (>5 ha) than big meadows (see Fig. 5).

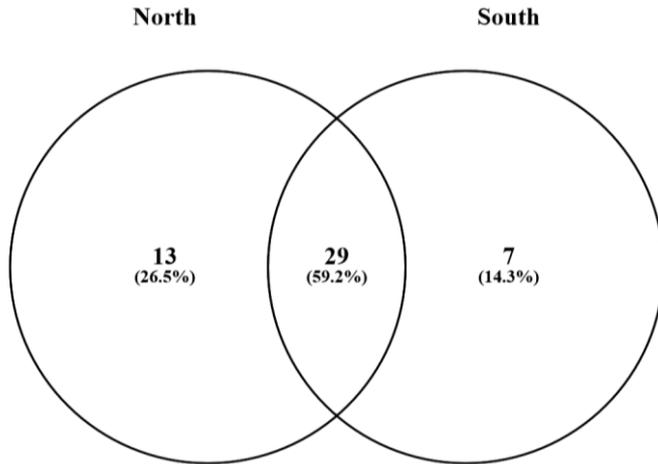


Figure 4: Species overlap between meadows located north and south of the levee, considering meadow-affiliated birds only.

Table 7: Total numbers of bird species recorded exclusively south and north of the levee as well as of species recorded on both sides of the levee.

Only south of levee	Ind.	On both sides of levee	Ind.	Only north of levee	Ind.
<i>Milvus migrans</i>	5	<i>Accipiter nisus</i>	6	<i>Anthus trivialis</i>	11
<i>Troglodytes troglodytes</i>	4	<i>Acrocephalus palustris</i>	15	<i>Phasianus colchicus</i>	7
<i>Prunella modularis</i>	3	<i>Aegithalos caudatus</i>	163	<i>Dryobates minor</i>	6
<i>Crex crex</i>	2	<i>Buteo buteo</i>	30	<i>Apus apus</i>	6
<i>Serinus serinus</i>	1	<i>Carduelis carduelis</i>	109	<i>Phoenicurus phoenicurus</i>	2
<i>Locustella luscinioides</i>	1	<i>Chloris chloris</i>	18	<i>Ardea cinerea</i>	2
<i>Regulus ignicapilla</i>	1	<i>Columba oenas</i>	3	<i>Ciconia nigra</i>	2
		<i>Columba palumbus</i>	47	<i>Acrocephalus arundinaceus</i>	1
		<i>Emberiza citrinella</i>	218	<i>Passer montanus</i>	1
		<i>Falco subbuteo</i>	5	<i>Phylloscopus trochilus</i>	1
		<i>Falco tinnunculus</i>	13	<i>Phoenicurus ochruros</i>	1
		<i>Ficedula albicollis</i>	108	<i>Coturnix coturnix</i>	1
		<i>Ficedula hypoleuca</i>	5	<i>Jynx torquilla</i>	1
		<i>Hippolais icterina</i>	31		
		<i>Hirundo rustica</i>	39		
		<i>Lanius collurio</i>	21		
		<i>Leiopicus medius</i>	31		
		<i>Merops apiaster</i>	29		
		<i>Muscicapa striata</i>	33		
		<i>Pernis apivorus</i>	11		

		<i>Phylloscopus collybita</i>	65
		<i>Picus viridis</i>	12
		<i>Poecile palustris</i>	38
		<i>Streptopelia turtur</i>	22
		<i>Sturnus vulgaris</i>	574
		<i>Sylvia atricapilla</i>	689
		<i>Sylvia communis</i>	2
		<i>Sylvia curruca</i>	4
		<i>Turdus merula</i>	66

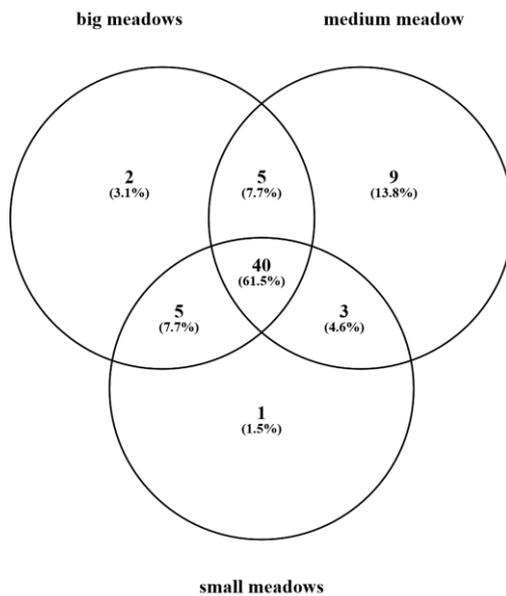


Figure 5: Overlap of species assemblages and species unique to meadows of different size classes (big meadows: >5 ha; medium-sized meadows: 2-5 ha; small meadows: <2 ha) only considering meadow-affiliated birds.

4.4 Nestedness

Calculated tests for nestedness (using BINMATNEST) indicate strongly nested bird assemblages, independently if all birds or only meadow-affiliated birds were considered (see Table 8).

The rank of meadows in the packed species-site matrix correlated positively with increasing meadow size for all bird species and meadow-affiliated birds (see Table 9.). Additionally, the ranks of meadow-affiliated bird assemblages as well as of all birds were positively related to forest edge length. Degree of isolation and distance to levee and density of the forest edge did not prove being significant related to meadow ranks extracted from the packed species-site matrix, whereas the ratio forest edge to meadow size was significantly correlated negatively with both matrices.

Table 8: Results of tests for nestedness of bird species assemblages, including only meadow-affiliated birds and including all birds recorded on sampled meadows. Given are temperatures of packed matrices and matrix temperatures according to null model 3.

	N° species	Temp _{Mat}	Temp _{Mod}	P
Meadow affiliated birds	48	23.49	41.74	<0.0001
Total birds	68	27.45	48.21	<0.0001

Table 9: Results of Spearman rank correlations relating site ranks in the packed (matrix calculated by BINMATNEST) to habitat variables. Significant relationships are printed bold.

Considered bird species	Meadow size	Ratio forest edge to meadow size	Meadow structures	Isolation	Distance to levee	Density of forest edge	Forest edge length
Meadow-affiliated birds	0.466*	-0.425**	0.265	-0.042	0.009	-0.103	0.468*
All birds	0.459**	- 0.491**	0.329***	- 0.034	0.057	-0.1468	0.437**

* $p < 0.001$; ** $p < 0.01$; *** $p < 0.05$ after FDR correction

4.5 Beta diversity

Multiple site dissimilarities β_{SIM} and β_{SOR} are similar between meadows north ($\beta_{SOR} = 0.85$ and $\beta_{SIM} = 0.79$) and south of the levee ($\beta_{SOR} 0.88$ and $\beta_{SIM} 0.79$). β_{SNE} indices are low on both sites of the levee demonstrating that nestedness only contributes little to overall beta diversity (Baselga 2010). The β_{ratio} was similar for both meadow-affiliated birds and all birds (see Table 10).

Table 10: The multiple-site Sørensen dissimilarity (β_{SOR}) and its components turnover (β_{SIM}) and nestedness (β_{SNE}) calculated for assemblages of meadow-affiliated birds considering all meadows and only meadows north and south of the levee, respectively, and considering all bird species and all meadows.

Considered bird species	Considered meadows	β_{SOR}	β_{SNE}	β_{SIM}	β_{ratio}^*
Meadow-affiliated birds	All	0.93	0.027	0.90	0.029
	North of levee	0.85	0.05	0.79	0.059
	South of levee	0.88	0.047	0.79	0.053
All birds	All	0.92	0.030	0.89	0.033

Results of dissimilarity indices were similar for meadow birds and total birds. β^x was high (all birds: 0.945; meadow-affiliated birds: 0.930) whereas β^+ was low (all birds: 0.0548; meadow-affiliated birds: 0.0702) indicating that bird communities do not vary much from site to site. β_T and β_N also don't show prominent differences between total birds ($\beta_T = 0.0348$, $\beta_N = 0.020$) and meadow birds ($\beta_T = 0.0382$, $\beta_N = 0.032$) and values were low for both sites.

4.4.1 Pairwise dissimilarities

Nestedness resultant component increased significantly with difference in meadow area ($r = 0.3609$, $p = 0.001$; Fig 6.) and differences of forest edge length ($r = 0.3314$, $p = 0.001$; Fig. 6), ratio forest edge to meadow site ($r = 0.1722$, $p = 0.001$; Fig. 6) and forest edge width ($r = 0.3321$, $p = 0.001$) for total birds. There were no significant turnover component for one of the habitat dissimilarities and no significant relations between hedges, forest edge density, meadow structures and pairwise dissimilarities whether for total birds nor for meadow birds. Overall relations of meadow-affiliated bird dissimilarities are quite similar to the ones of all birds as the nestedness component seems to explain best meadow size ($r = 0.2984$, $p = 0.001$), forest edge length ($r = 0.2229$, $p = 0.001$) and ratio of forest edge to meadow size ($r = 0.1723$, $p = 0.003$).

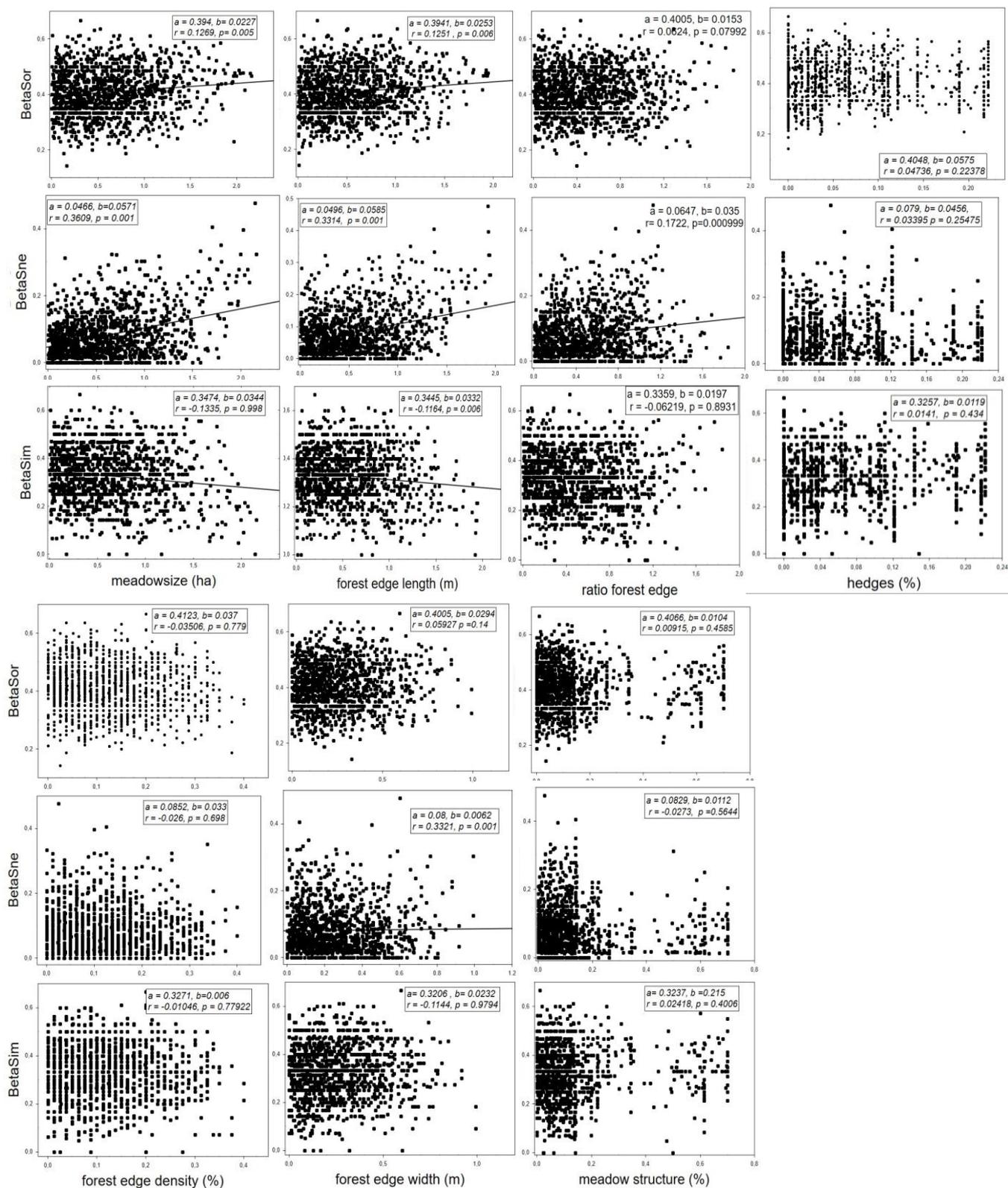


Figure 6. Relationships of overall beta diversity (Beta sor) and its components of turnover (BetaSim) and nestedness (BetaSne) with differences in meadow size, forest edge length, ratio forest edge, forest edge density, forest edge width and meadow structures calculated by considering all bird species.

Abbreviations: slope of multiple regression model, a; intercept of multiple regression model, b; Pearson correlation coefficient, r = regression coefficient; p-value of Mantel permutation test.

5. Discussion

5.1 Species richness

Our results indicate that larger meadows harbor more bird species and individuals than smaller meadows as it was shown by previous studies (Helzer & Jelinski 1999, Besnard & Secondi 2014). This can be explained by the area sensitivity of birds (Vickery *et al.* 1994, Helzer & Jelinski 1999, Davis 2004) according to the ecological concept of the species-area relationship, which assumes that the species richness increases with increasing area (Usher & Erz 1994, Coner & McCoy 2013). In addition, larger areas tend to provide more habitats than smaller ones (Worthen 1996). The negative correlation between species richness and the ratio forest edge to meadow size again indicates high species sensitivity to area size (Ambuel and Temple 1983, Howe 1984), rather than forest edge length. An increasing ratio means a higher complexity of the meadow shape. Consequently meadow core areas decline and the importance of edge effects is increasing and hence contributing to the recorded avifaunal richness. Additionally, results reveal that large meadows play significant role for raptors. They represent important feeding sites for species such as European Honey Buzzard, Eurasian Hobby and Common Kestrel (Limbrunner *et al.* 2013). and breeding habitats for Black Kites which preferentially build its eyrie in trees located at forest margins (Glutz von Blotzheim 1985). Summarizing, we can say that meadow size is the best explanatory variable for differences in bird species richness and abundance.

5.2 Indicator species

We could not find indicator species for regularly flooded meadows south of the levee but north of the levee. Furthermore we could determine indicator species for different categories of meadow size. The absence of indicator species regarding flooded meadows indicates that habitat requirements do not vary much between northern and southern sites (de Cáceres & Legendre 2013). Common Pheasant, a frequent species of surrounding farmlands was only recorded north of the levee probably due to proximity of northern sites to agricultural land (Limbrunner *et al.* 2013). Surprisingly the Lesser-spotted Woodpecker, a species which prefers willows and poplars of the soft-wooded floodplains was also determined as indicator species for northern sites. As we only counted six individuals of this species we assume that the insufficient data may bias our results. Common Bee-eater, Common Buzzard, Common Kestrel, Red-backed Shrike and Yellowhammer were detected as indicator species of larger meadows. Common Bee-eaters may be attracted to floodplain forest areas because of a generally high abundance of flying insects. Therefore bigger meadows possibly provide better food requirements. In case of the raptors Common Buzzard and Common Kestrel large meadows offer more space for hunting flights over the ground and facilitates

maneuverability for launching and landing. Furthermore, large open areas are easier to overview and therefore reduce predation risks. The abundance of other species is also increasing with meadow size (e.g. such as Yellowhammer) or the length of forest edges (e.g. Eurasian Blackcap). Moreover, some species depend on certain meadow structures, as indicated by the relationship between the occurrence of Red-backed Shrike and hedges.

5.3 Nestedness, beta diversity and species turnover

Bird communities proved being significantly nested. At this point it should be noted that nestedness temperature can reflect habitat specificity and is considered to be lower (more nested) with ascending specificity of birds and vice versa (Wright *et al.* 1998). Hence a lower matrix temperature of meadow-affiliated birds reflects higher specificity of the bird communities compared to the assemblage of all birds. The pattern of nestedness was closely related to changing meadow size with species poor bird communities of smaller meadows representing subsets of species rich communities of larger meadows (Patterson *et al.* 1986). These results correspond with the nested habitat hypothesis (Worthen 1996), which claims that sites with few habitats (e.g. smaller meadows) are subsets of sites with many habitats (e.g. larger meadows). Hence, the loss of species with decreasing meadow size could be the result of a nested habitat quality (Worthen 1996, Lindenmayer *et al.* 2002).

Meadow structures i.e. are so called quality variables (Hylander *et al.* 2005) for birds as communities are nested according meadow structures revealing that meadows with more meadow structure coverage host species richer bird communities than meadows with lower coverage of meadow structures. This is supported by the documented increase of species richness with an increase in meadow structures, underlining a positive response of bird assemblage richness to meadow structures (Davis 2004, Nikolov 2010, Besnard *et al.* 2014). Remarkably, Baselga's (2010) multiple dissimilarity indices indicated a very low contribution of nestedness to overall beta diversity. However, this conclusion that beta diversity is predominantly caused by species turnover can be misleading (Almeida-Neto *et al.* 2008, Almeida-Neto *et al.* 2012, Ricotta and Pavoine 2015, Ulrich *et al.* 2017) because β_{SNE} decreases with matrix size. Furthermore, this measure does not necessarily have to increase with nestedness (Ulrich *et al.* 2017) because it is depending on matrix filling. Ulrich *et al.* (2017) found out that matrix filling influences dissimilarity measures as β_{SNE} decreases with high filling. Using Ricotta's indices, it becomes clearer that species communities among sites are very similar (high β^*) and turnover plays minor role in shaping bird species communities (low β^T). Overall nestedness analysis lead to the conclusion that sites are homogenous regarding species composition which can be explained by a high dispersal ability of birds as a result of absence of barriers (Ricotta and Pavoine 2015) and high spatial connectivity of

sites (Tonkin *et al.* 2016). Meadow size is the best environmental predictor variable for explaining the nested metacommunity organization.

5.4 Conservation aspect

Our results show that meadows were rarely visited by raptors (despite European Honey Buzzard) or other larger birds of high conservation interest. We made two observations of Black Storks at Stockmais meadow. For this species it is important maintaining meadows of high wetland character (Glutz von Blotzheim 1985, Jiguet & Villarubias 2004), which are preferentially used as foraging habitat. Furthermore it is recommended to keep human disturbance as low as possible by abandonment of trails because the Black Stork is relatively sensitive to human disturbance (Glutz von Blotzheim 1985, Chevallier *et al.* 2010). Five observations have been made of the Black Kite, a species which has 10-20% of its Austrian breeding population in the DNAP (IBA criteria C6, Dvorak & Berg 2009). Although we assume that meadows only play a minor role as foraging habitat as the species primarily feeds on fish (Glutz von Blotzheim 1985), tall strong trees at forest margins harboring potential nest sites may represent an important habitat requisite. Considerable attention has to be given to the Tree Pipit which was known to be a frequent breeding bird of meadows in the DNAP (Dvorak & Berg 2009) but population declines have been recorded in DNAP. We only made observations on two meadow sites of this ground breeding species and suspect that early mowing regime does have negative impact on the population in the DNAP.

We recommend the maintenance of large extended meadows as they facilitate higher bird species richness more than smaller patches. To support populations of larger birds in the National Park Donau-Auen such as Black Stork and raptors like Black Kite and European Honey Buzzard large meadow patches have to be maintained as they are used as feeding sites (Frühauf & Wichmann 2006). Formerly, the Corncrake had been a frequent species in the wetland meadows of the Danube river floodplains (Von Österreich & Brehm 1879) but suffered severe declines in the 20th century on a global scale. In 1999 only three territories have been recorded in the National Park Donau-Auen (Frühauf 2006) and in 2016 only two territories have been found (Christina Nagl, personal communication). Despite recommendations for a late mowing (in July) of all big meadows (> 5 ha) (Frühauf & Wichmann 2000), in 2016 these meadows were mowed already in May (own observation). Maintenance of structures such as hedges and stopping further vegetation succession on meadows would be of advantages for the Red-backed Shrike which depends on hedges as nesting sites and adjacent open areas for hunting on larger arthropods (Glutz von Blotzheim 1985). Common species as Common Starling and Yellowhammer tend to occur on a large proportion of meadows (see Appendix 1). In contrast, rare species (e.g. recorded with <5

individuals), such as Common Quail, Corncrake, Black Stork, Black Kite and Eastern Imperial Eagle, tend to occur only at meadows bigger than 3 ha. Small meadows show similar bird assemblages as they are very monotonous regarding structural availability. We suspect edge effects to be too dominant in small meadows to facilitate the occurrence of meadow-affiliated bird species. Loss of large meadow patches and progressing vegetational succession on meadows seems to be the main driver of open land bird species loss (Wichmann & Frühauf 2000).

To summarize, future management measures should target conserving big meadows, supporting diversification respectively meadow structures and to create mosaic pattern of habitats.

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Appendix 2. Species richness and habitat variables at sites

Meadows	Total species richness	Species richness of meadow affiliated birds	log(Meadow area (ha) +1)	log (ratio forest length to meadow size)	log (length of forest edge)	log (forest edge width (m) +1)	single trees (%)	hedges (%)	bushes (%)	reed (%)	tall forbes (%)	total meadow structures (%)
N01	19	10	0.947789399	6.31106836	6.76849321	2.29000631	0.00	0.00	0.00	0.00	0.00	0.000
N02	34	21	2.61483782	5.34723912	7.8860814	2.22462355	0.02	0.12	0.16	0.00	0.00	0.138
N03	16	7	0.54696467	6.56162113	6.2441669	2.57451881	0.01	0.00	0.00	0.00	0.00	0.007
N04	22	14	0.643956936	6.76660964	6.66568372	2.50552594	0.00	0.22	0.00	0.40	0.00	0.615
N05	16	9	0.867100488	6.17770354	6.49978704	2.37490575	0.03	0.00	1.38	0.04	0.00	0.083
N06	20	11	0.734289124	6.69584909	6.77650699	2.43798973	0.00	0.22	0.00	0.08	0.04	0.345
N07	23	12	1.38629436	5.91350301	7.01211529	1.83258146	0.00	0.19	0.77	0.00	0.03	0.222
N08	23	11	1.22964055	6.3955513	7.27931884	2.33939907	0.00	0.04	0.70	0.06	0.01	0.121
N09	17	12	0.526502103	6.36566184	5.99893656	2.30258509	0.00	0.00	0.00	0.00	0.03	0.036
N10	18	11	1.42310833	5.79957354	6.94697599	2.32727771	0.00	0.00	0.00	0.00	0.00	0.000
N11	20	13	1.7119945	5.70963901	7.22256602	1.9980959	0.00	0.11	1.67	0.00	0.00	0.123
N12	25	16	1.46787435	5.94080137	7.14677218	2.06305806	0.01	0.03	0.00	0.00	0.05	0.090
N13	22	13	1.20896035	5.58812484	6.44254017	2.62103882	0.09	0.01	0.00	0.00	0.09	0.199
N14	18	9	1.38379123	5.8517026	6.94697599	2.19722458	0.02	0.00	0.00	0.00	0.11	0.132
N15	16	7	1.95444505	5.08277685	6.88448665	2.22462355	0.00	0.00	0.07	0.00	0.00	0.004
N16	16	8	0.815364813	6.40483483	6.63594656	2.01490302	0.00	0.00	0.00	0.00	0.00	0.000
N17	17	11	1.16938136	6.13980689	6.93731408	2.1690537	0.00	0.00	0.00	0.00	0.00	0.000
N18	22	15	2.02946317	5.59578499	7.48436864	2.07944154	0.00	0.07	0.00	0.00	0.00	0.070
N19	18	11	1.81319475	5.65108606	7.28619171	2.32042501	0.00	0.06	0.00	0.00	0.00	0.056
N20	17	11	0.858661619	6.13186567	6.43935037	1.98100147	0.02	0.00	0.00	0.00	0.00	0.017
N21	19	11	1.18478998	5.93947544	6.75925527	2.59301339	0.03	0.03	0.00	0.00	0.00	0.058
N22	19	10	1.26129787	5.96238982	6.89060912	2.61190634	0.00	0.01	0.00	0.00	0.00	0.009
N23	12	7	0.470003629	6.47697236	5.96614674	2.82583324	0.05	0.07	0.00	0.00	0.00	0.115
N24	17	7	0.916290732	5.78894028	6.19440539	2.12525108	0.00	0.00	0.00	0.00	0.00	0.000
N25	28	17	1.53471437	5.50372209	6.79570578	2.27726729	0.01	0.09	0.00	0.00	0.00	0.101
S01	17	10	1.66581825	5.69832862	7.15461536	2.19722458	0.02	0.00	0.00	0.00	0.00	0.000
S02	22	13	1.84371921	5.77277535	7.44424865	2.46385324	0.00	0.00	0.00	0.00	0.00	0.000
S03	14	10	0.456791735	6.50229017	5.95583737	2.15466496	0.04	0.00	0.00	0.00	0.00	0.036
S04	14	7	0.819779831	6.52023837	6.75925527	2.1102132	0.05	0.00	0.00	0.00	0.00	0.000
S05	16	10	0.635518068	6.21685782	6.09807428	1.83258146	0.01	0.00	0.00	0.00	0.00	0.000
S06	22	11	1.41098697	5.50847372	6.63987583	1.94591015	0.00	0.00	0.00	0.00	0.00	0.000
S07	25	15	1.62136648	5.3718974	6.77308038	2.23804657	0.06	0.00	0.22	0.00	0.00	0.060
S09	21	11	1.92716411	5.63867593	7.40853057	2.14006616	0.03	0.14	0.12	0.00	0.00	0.170
S10	22	10	1.67896398	5.55750085	7.02997291	2.14006616	0.00	0.10	0.30	0.00	0.00	0.111
S11	20	12	2.05923883	5.56718317	7.4899709	2.1102132	0.07	0.04	0.00	0.00	0.00	0.102
S12	21	14	1.31372367	5.66632491	6.66695679	2.29000631	0.00	0.00	0.00	0.00	0.00	0.000
S13	18	11	2.29253476	4.92871817	7.11476945	2.19722458	0.02	0.06	0.00	0.00	0.00	0.084
S14	16	10	1.28093385	6.13456539	7.09007684	2.12525108	0.02	0.00	3.12	0.21	0.00	0.262
S15	22	12	1.69744879	5.57812095	7.07326972	2.1102132	0.10	0.00	0.20	0.00	0.00	0.104
S16	15	9	0.616805947	6.10703072	5.94803499	2.48490665	0.06	0.00	0.00	0.00	0.00	0.001
S17	16	10	1.12167756	5.6021723	6.32972091	2.19722458	0.01	0.11	0.00	0.00	0.00	0.121

S18	21	12	1.01160091	5.86200648	6.42162227	2.1690537	0.02	0.00	0.00	0.00	0.00	0.000
S19	14	7	0.91228271	6.12037117	6.51914729	2.29000631	0.03	0.00	0.00	0.00	0.00	0.000
S20	21	12	0.712949808	6.13456539	6.1737861	2.48490665	0.00	0.02	0.00	0.00	0.00	0.000
S21	22	11	1.36353737	5.43763098	6.50578406	1.94591015	0.06	0.04	1.92	0.00	0.58	0.701
S22	22	12	1.01160091	6.41579814	6.97541393	2.7488722	0.02	0.00	0.00	0.00	0.00	0.031
S23	17	9	1.4632554	5.66800963	6.86797441	2.54553127	0.01	0.01	0.24	0.00	0.00	0.021
S24	16	10	0.660623989	6.23575053	6.16961073	2.35137526	0.08	0.00	0.00	0.00	0.11	0.186
S25	22	13	1.43746265	5.54181315	6.70808408	2.27726729	0.12	0.02	0.00	0.00	0.00	0.141
S26	31	17	2.49320545	5.48662697	7.89357207	2.37490575	0.04	0.00	0.04	0.00	0.00	0.044