universität
wien

DIPLOMARBEIT / DIPLOMA THESIS

Titel der Diplomarbeit / Title of the Diploma Thesis

„Spatio-temporal patterns of dragonfly occurrence on meadows in the national park Donau-Auen, Lower Austria“

verfasst von / submitted by

Natascha Wild

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of

Magistra der Naturwissenschaften (Mag.rer.nat.)

Wien, 2017 / Vienna, 2017

Studienkennzahl lt. Studienblatt / degree programme code as it appears on the student record sheet:	A 190 445 344
Studienrichtung lt. Studienblatt / degree programme as it appears on the student record sheet:	Lehramtsstudium Biologie und Umweltkunde UniStG Lehramtsstudium Englisch UniStG
Betreut von/ Supervisor:	Ass.-Prof. Dr. Christian H. Schulze

Acknowledgements

I wish to express my gratitude to Dr. Christian H. Schulze for his valuable guidance and support as part of his role as my supervisor. The completion of this project would not have been possible without his helpful advice, his constructive feedback and his support in statistical matters.

I sincerely thank the Donau-Auen National Park team for their cooperation and support. I particularly would like to thank Stefan Schneeweihs for sharing his experience in working with dragonflies and damselflies and providing his help in selecting representative sampling sites for this field work. I would like to thank Karoline Zsak for providing all necessary information about the Donau-Auen National Park I required, in order to being able to carry out this project. Moreover, I am thankful to Dr. Christian Baumgartner for enabling this field work.

I express deep and sincere gratitude to my fellow student friends, Tatjana Knaus, Cornelia Holzer, Marina & Lena Stehlik and Andrea Gschöttner who supported and encouraged me endlessly during the course of my studies and who spent numerous exciting field trips with me, exploring nature.

Finally, I am thankful to Michael Widy and my entire family for their immense support during this time and their endless patience.

Map data copyrighted OpenStreetMap contributors and available from https://www.openstreetmap.org.

Table of Contents

Zusammenfassung

Spatio-temporal patterns of dragonfly and damselfly occurrence on meadows in the National Park Donau-Auen, Lower Austria

Die Dispersionsfähigkeit ist ein charakteristisches Merkmal immaturer und adulter Libellen. Während das Ausbreitungsverhalten von Libellen innerhalb von Gewässern bereits intensiv erforscht wurde, hat die Ausbreitung zu terrestrischen Habitaten, zum Zweck der Nahrungssuche, bislang nur wenig Beachtung gefunden.

Diese Studie zielte darauf ab, das Ausbreitungsverhalten adulter Libellen von Gewässern zu nahegelegenen Wiesen zu untersuchen, welche zur Nahrungssuche und als Rastplatz genutzt werden. Dazu wurden Libellen zwischen Mai und September 2016 auf 16 Wiesen und zusätzlich an acht Gewässerstandorten im Nationalpark Donau-Auen im Bereich Orth an der Donau erhoben. Insgesamt wurden 1.427 Libellen beobachtet, wovon 667 Individuen auf Wiesen vorkamen und 29 Arten (11 der Unterordnung Zygoptera, 18 der Unterordnung Anisoptera) nachgewiesen wurden.

Anisoptera zeigten generell eine größere Neigung, nahegelegene Wiesen zu nutzen als Zygoptera; Weibchen zeigten verhältnismäßig höhere Abundanzen auf Wiesen als am Gewässer. Die Distanz zu nahegelegenen Gewässern hatte einen signifikanten Einfluss auf das Vorkommen, den Artenreichtum und die Artenkomposition von Libellen auf Wiesen. Darüber hinaus zeigte sich eine große Bedeutung der Struktur angrenzender Waldsäume an Wiesen auf das Vorkommen bestimmter Arten.

Die Ergebnisse dieser Studie liefern somit einen wichtigen Einblick in die Nutzung von in Auenwälder eingebetteten Wiesen durch adulte Libellen.

Abstract

Dispersal is a characteristic trait in Odonata. While dispersal behaviour of dragonflies and damselflies between waterbodies has generally received a great deal of attention, dispersal processes subjected to terrestrial habitats and hence, Odonate's use in the context of foraging activities, have previously only attracted limited interest. This study aimed to investigate the dispersal of dragonflies and damselflies to meadows used for foraging or as refuge. The primary focus was on assessing species-specific dispersal characteristics influencing the spatial distribution of species, species richness and community structure on meadows. Therefore, dragonflies and damselflies were sampled between May and September 2016 at 16 meadow and eight waterbody sites in the Donau–Auen National Park (DANP), Eastern Austria near Orth an der Donau.

In total, 1.427 dragonflies were recorded, including 667 observed on meadows. Anisopterans were more likely to disperse long distances from waterbodies than zygopterans, and females showed proportionally higher abundances on meadows than at waterbodies. Species composition, species richness and occurrence of dragonflies were highly influenced by the distance meadows were situated away from waterbodies. Moreover, the results from this study demonstrated that occurrence of Odonata, species richness and the structure of species assemblages are associated with structural characteristics of forest margins adjacent to meadows. For most Odonata species, a positive relationship between heterogeneity in forest margin vegetation structure and occurrence could be found.

This study provides important insight into odonate's utilization of meadows embedded in floodplain systems and provides some basis for potential conservation management considerations with the aim to protect terrestrial habitats of rare dragonflies.

Introduction

The key role of Odonata (dragonflies and damselflies) as bioindicators for habitat quality has been highlighted in numerous studies (Chovanec, 1999; Chovanec, et al., 2004; Clark & Samways, 1996; Corbet, 1999; Raab, 2000; Schulz, 2006; Schmidt, 1985). However, ecological studies on adult dragonflies and damselflies tend to concentrate on their aquatic habitats and the adjacent terrestrial transition zone (Buchwald, 1989; Chwala & Waringer, 1996; Lenz, 1991; Schindler, et al., 2003; Raab, 2000; Wildermuth, 1994). Spatial movements to non-aquatic foraging habitats situated in larger distances to the larval habitats have received little attention. Various studies focused on the dispersal of Odonata, as a response to seasonal changes or movements between neighboring waterbodies (Conrad, et al., 1999; Parr, 1973; Stetter, 1996; Thompson, 1991). In contrast, dispersal to distanced meadows for the purpose of foraging, mate-seeking, pairing or seeking of refuge has been scarcely investigated (Conrad, et al., 1999; Hykel, et al., 2016; Rouquette & Thompson, 2007).

In this study, we assessed the importance of meadows, embedded in a river-floodplain system, as foraging habitats for adult Odonata. So far, research of dragonflies and damselflies in river-floodplain systems in Austria largely focused on the effect of lateral hydrological connectivity of floodplain channels on the occurrence of species (Chovanec & Waringer, 2001; Chovanec, et al., 2004; Raab, 2000; Schneeweihs, 2016). Also, environmental factors determining the preference of species for aquatic breeding sites have been subject to scientific research (Staufer & Schulze, 2011; Tockner, et al., 1999). However, little is known about the importance of floodplain meadows for Odonata (Conrad, et al., 1999).

Dispersal plays an integral part in odonate life and can be prompted by several motivators. Taylor (1986) provides a functional definition of dispersal in Odonata and distinguishes three major types of dispersal: (a) Maiden flight, occurring shortly after emergence, (b) commuting, which includes movements between roosting, foraging and reproductive sites and (c) seasonal refuge, movements to alternative reproductive sites as a response to seasonal changes rendering waterbodies uninhabitable. This study is primarily concerned with movements that fall into the first and second category, which according to Corbet (1999) entails movements between 10 m to several kilometers.

Dragonflies and damselflies regularly undertake routine movements from and to waterbodies as part of their foraging activities (Corbet, 1999; Kirkton & Schultz, 2001; McPeek, 2008).

Typically, adults in their teneral stage fly away from their natal site immediately after emergence and do not return until reproductively mature, often many days later (Corbet, 1980). It is primarily assumed that they perform these dispersal movements to avoid sexually mature males (Corbet, 1999). Hence, teneral dragonflies are assumed to be the primary group of dragonflies involved in dispersive processes (Conrad, et al., 1999). Female dragonflies spend considerable time outside their aquatic environments and visit waterbodies predominantly to mate and oviposit (Corbet, 1999; McPeek, 2008; Moore, 1954; Suhonen, et al., 2008; Wildermuth, 2012). Another driver for dispersal from breeding sites is escape from or avoidance of harassment of males by females as a consequence of excessive mating attempts at reproductive sites (Marden & Rowan, 2000). A male-biased sex ratio at breeding sites is therefore assumed (Suhonen, et al., 2008). To date, we lack sufficient insight about sex-specific differences in the use of feeding habitats (Suhonen, et al., 2008). Other studies account interspecific aggression for dispersal to less preferred habitats by individuals of subdominant species (Moore, 1964; Tynkkynen, et al., 2008). Moreover, the use of terrestrial environments for nocturnal roosting, is another driving factor causing dragonflies to disperse from their aquatic habitats (Rouquette & Thompson, 2007). Dispersal can also be motivated by reproductive activity at rendezvous or fulfill thermoregulatory purposes (Corbet, 1999). Distances moved between roosting sites and rendezvous are typically influenced by local topography and vegetation and can range from a few centimeters to several hundred meters depending on the species (Corbet, 1999; Moore, 1954).

Research available about dispersal is often derived from analysis of population density, providing rather indirect evidence of dispersal (Conrad, et al., 1999). Quantifying dispersal is difficult (Angelibert & Giani, 2003) and studies on dispersal are often associated with capture-mark-recapture studies, making it only possible to include few species in a study. A recent study conducted in the Czech Republic investigated dispersal of *Sympetrum depressiusculum* in a primarily agricultural area with remnants of floodplain forest and meadows, featuring five farm ponds where this species occurs. The study was interested in the effect of distance from the species' natal site on its abundance in terrestrial habitats, sex-specific differences in terms of terrestrial habitat use and structural vegetation demands on their terrestrial habitat. They found that abundance of *S. despressiusculum* was significantly lower in more remote sampling patches. The study could not confirm that distance from the natal site has a sex-specific effect on the abundance of males and females (Hykel, et al., 2016).

A capture-mark-recapture study examined dispersal characteristics of *Coenagrion puella*, *Coenagrion scitulum* and *Libellula depressa* in a patchy habitat in southwest France. The study reports sex- and age-specific differences in dispersal ability and showed that anisopterans were more likely to disperse than zygopterans (Angelibert & Giani, 2003).

Although the dragonfly fauna of the DANP has been subject to previous studies (Chovanec & Waringer, 2001; Raab, 2000; Schulz, 2006), little is known about dragonflies' usage of meadows. This study primarily aimed at identifying spatial patterns in species distribution and species composition of adult dragonflies on meadows in the DANP to draw conclusions about their dispersal behavior. Moreover, a central goal of this study was to explore how structural quality of terrestrial habitats affects dragonfly occurrence, species richness and the structure of dragonfly communities.

In particular, we addressed the following questions:

(1) Are species composition, species richness and abundance influenced by the distance meadows are situated away from waterbodies?

Due to dragonflies' and damselflies' varying flying ability, we expect that abundance of Anisoptera species is still high at meadows which are located at larger distances to waterbodies, while abundance of Zygoptera is expected to be greater at meadows which are more closely situated to waterbodies (Corbet, 1999). Moreover, we expect a shift in species composition at meadows with increasing distance to waterbodies. With respect to odonate's habitat specificity - some species prefer lentic or lotic water habitats or require specific vegetation for oviposition - we also expect that meadows located at great distance from waterbodies are more likely to be visited by habitat generalists since the chance of finding a suitable aquatic habitat is greater for such species (Corbet, 1980). Furthermore, we also assume a female-biased sex-ratio on meadows since females are described to spend most of their adult life away from aquatic habitats as a result of harassment by males (Corbet, 1999; Suhonen, et al., 2008).

(2) Are species composition and species richness of Odonata species influenced by the structural quality of forest margins on floodplain meadows?

Densely branched trees, shrubs and meadows covered with tall grass provide perching opportunities for odonates between foraging flights and provide shelter between periods of high wind, rain or dense cloud cover (Corbet, 1999). Therefore, we expect that species composition and species richness are influenced by structural characteristics of meadows. Since structural demands on habitats vary between Odonate species (Dijkstra, 2014), it is assumed that species richness is higher at meadows characterized by structurally diverse forest margins. Moreover, species composition is expected to differ between structurally diverse and structurally uniform vegetation.

(3) Is Odonate abundance influenced by prey availability?

We expect that abundance of Odonates correlates with prey availability. Odonates were described to forage in high abundances at habitats were potential prey is abundant (Kirkton & Schultz, 2001).

Material and Methods

Study area

The Donau-Auen National Park (DANP) is an accredited Riverine Wetlands National Park (IUCN Category II, 1997) covering an area of 9,300 hectares along the river Danube, ranging from Vienna to Bratislava. It represents the largest ecologically still functional riparian ecosystem in Central Europe. DANP's landscape is characterized by 65% riparian forest, 20% waterbodies and 15% meadows (Nationalpark Donau-Auen, 2011-2017).

Owing to annual water level fluctuations of the river Danube, the adjacent floodplains are influenced by regular flooding events. Water level peaks in early summer as a consequence of early summer precipitation climaxes and water level fluctuations caused by snowmelt in the Alps lead to flooding events in the DANP from late spring to high summer (Tockner, et al., 1999). The construction of a levee in the 1970s, that protects the inhabited area around the Danube river against flooding, led to the development of relatively dry meadows north of the levee, which are only affected by rising groundwater during high water levels of the Danube. In contrast, the nutrient-rich riparian meadows south of the Marchfeld levee are still regularly flooded (Nationalpark Donau-Auen, 2011-2017).

Meadows of the DANP are subject to management measures regulated by an agreement (in accordance with Article 15a) between the federal constitution and the provinces of Lower Austria and Vienna, developed for the establishment and maintenance of the Donau-Auen National Park (NÖ Nationalparkgesetz, LGBI. 5505/1 §6 Managementplan). One of its primary goals is to preserve rare meadow types and its structural elements that are vital for the preservation of birds, insects and other animals. Management of meadows entails regular mowing to prevent shrub encroachment and to preserve the diversity of meadows. Mowing of meadows in the DANP is regulated through contractual conservation management agreements with third parties. Mowing is done once or twice a year, in June and August (Nationalpark Donau-Auen, 2009).

Study sites

This study was conducted in the Eastern part of the DANP north of the Danube river in the area of Orth an der Donau (48° 9′ N, 16° 42′ E). A levee (Marchfeldschutzdamm) divides the study area into a northern part, an area that is protected against flooding events during periods of high water levels and the southern part, an area that is regularly flooded due to summer inundations.

A total of 16 meadows were sampled from the beginning of May until September. Six study sites were situated in the northern part of the area, seven sites were situated south of the Marchfeld levee and three study sites were located directly on the Marchfeld levee. Eight waterbody sites alongside Danube River's side arms and one lentic waterbody in the northern part of the study area were selected as reference sites (Figure 1). Survey sites were randomly selected according to distance to waterbodies north and south of the Marchfeld levee. Only meadows that are subject to the current management plan of the DANP were included in the study (Nationalpark Donau-Auen, 2009). Detailed information about sampling sites can be found in the appendix A1-2.

Figure 1. Map of the study area indicating sampled meadows (M) and waterbody sites (W). Different coloration indicates waterbodies (blue), forest (green) and meadows (yellow).

Survey method

Sampling of dragonflies

On each meadow, adult Odonata were sampled by slowly walking along 100 m transects placed close to the forest margins. All dragonflies and damselflies encountered within a 10m radius of walking direction were counted. Reference data was collected at waterbodies by sampling stretches of 50 m along river banks. All adults observed on the bank and over the waterbody were recorded.

Field collections were performed between 10:00–16:00 CEST (Schindler, et al., 2003) when dragonflies are most active. Surveys lasted between 30 and 40 minutes at each site. Sampling was performed on sunny days with low or no wind. To cover all phenological groups of Odonata, each sampling site was visited 7 times, spread over the flight season from May to September (Schmidt, 1985). Influence of daytime on sampling results was avoided by systematically changing the daytime a site was visited (Chovanec, 1999).

Dragonfly and damselfly specimens were observed with binoculars (10 x 40) or caught with a sweep net (diameter: 40 cm) and identified by sight or photographs (Schindler, et al., 2003) using identification keys of Bellmann (2013) and Dijkstra (2014). Caught dragonflies and damselflies were released immediately after identification.

Habitat parameters on meadows

In order to determine dispersal distances of Odonata to surrounding terrestrial habitats, meadows were located at varying distances from waterbodies. Distances between meadows and waterbodies were measured using QGIS (version 2.18.4) and ranged from 95 to 1205 meters.

Structural diversity of meadows was categorized based on the availability (presence or absence) of "big trees", "small trees" and "shrubs". Sites were then assigned to three categories, category 3 representing sites were all three variables were present, category 2 and 1 represent sites were two and one variable were present, respectively, resulting in a categorial structural diversity index ranging from 3 (diverse) to 1 (uniform), hereinafter referred to as 'SDIa'.

Additionally, we quantified structural complexity of forest margins. Therefore, the length of the forest margin of each site was measured along the 100 m transects using a measuring tool implemented in the programme GoogleEarth version 7.1.8.3036). Values of the calculated lengths of forest margins were then divided by the length of the 100 m transects. Resulting index values ranged from 1-1.15, hereinafter referred to as 'SDIb'. Detailed information about structural diversity of meadows can be found in the appendix (Table A2).

In order to quantify the height of the herb layer on meadows, vegetation height was measured at nine points along each 100 meter transect, one every ten meters. The first measurement was taken at ten meters from the starting point, the last was taken at 90 meters from the starting point. A measuring tape was used to measure the height of the herb layer. Measurements were done at each of the seven visits. The mean of all nine measurements taken per visit was calculated and used for further analysis.

Abundance of potential prey was estimated using binoculars adjusted to focus a reference point in 10 m distance. Abundance of Odonata prey was then assessed by slowly screening from left to right in a semi-circle for 45 seconds and counting all flying insects that could be observed.

Table 1 provides a summary of all habitat variables, measured at meadows.

Table 1. Variables assessed for each sampled meadow transect. Variable 1 was measured using QGIS version 2.18.4. Variable 2 is based on estimation. Variable 3 was measured using GoogleEarth version 7.1.8.3036. Variable 5 is based on a count of flying insects. (*) measured at each visit.

No.	Variables	Units of measurement
1	Distance to closest waterbody	Meters
2	Structural diversity index (SDIa)	3 categories: (1) uniform to (3) diverse
3	Structural diversity index (SDIb)	length of forest margin in m/100 m
4	Height of herb layer	mean of 9 measuring points along transect*
5	Prey availability	45 sec. count of flying insects*

Data analysis

Statistical analyses were computed using the free software R, version 1.0.136 (R, 2013). Datasets were tested for normal distribution and *log, sqrt* or *arcsin-square-root* transformed if necessary. Statistical significance was established using $\alpha = 0.05$.

Species richness

Species richness estimates were calculated for all sample sites using the programme EstimateS 9.1.0 (Colwell, 2013). Sample order was randomized 100 times. Species richness estimates of meadow and waterbody sites were extrapolated to enable comparison of species accumulation curves (Colwell, 2013). Pearson's product-moment correlations were calculated to test if species richness was related to the distance from a waterbody and SDIb. In order to test for effects of structural diversity of the forest margin (SDIa) on species richness, a one-way ANOVA model was used.

Abundance

Pearson's product-moment correlation was applied to test if the number of individuals is correlated with the distance to a waterbody. The same model was used to test for correlation between the number of individuals and structural diversity of the forest margin (SDIb). A Kruskal-Wallis rank sum test was used to examine the relationship between Odonata abundance and SDIa. The corresponding post-hoc test Kruskal-Nemenyi, implemented in the package PMCMR, was used for pairwise comparisons. Moreover, influence of prey availability and the mean height of the herb layer on the number of dragonflies and damselflies was tested using a Spearman's rank correlation.

Species composition

Bray-Curtis similarities were computed using Primer v7 (Clarke & Gorley, 2015) to quantify similarity in species composition of sampling sites. Non-metric multidimensional scaling plots (NMDS) were used to visualize similarity relationships between sites. Therefore, sites were assigned to three categories based on their proximity to waterbodies (0-250m, >250-500m, >500m). In order to test for the effect of distance from a waterbody on species composition (Bray-Curtis similarities), Pearson's product-moment correlations were used to relate Dimension 1 and Dimension 2 values, extracted from the NMDS ordination, to distances of meadows to the nearest waterbody. Further, one-way ANOSIMs were used to test for the effects of structural variables and distance from waterbodies (classified as 0-250m, >250-

500m, >500m) on species composition. Corresponding post-hoc tests allowed pairwise comparisons.

Species-specific dispersal distances

The free programme QGIS 2.18.4 was used to produce maps of the study area, visualizing the distribution of recorded dragonfly species. Abundance data of all seven visits were summarized per species and ten abundance classes were established for visualization (0, 1-10, 11-20, 21-50, 51-70, 71-100, 101-130, 131-200, 201-240 counted individuals). To be able to compare waterbodies and meadows, abundances of waterbodies were multiplied by two.

Results

In the course of this study, a total of 1.427 dragonflies and damselflies were recorded, belonging to 29 species (Zygoptera: 11 species; Anisoptera: 18 species) and 8 families (Zygoptera: 4 families; Anisoptera: 4 families). At meadow sites, 667 individuals representing 20 Odonata species were counted. Six Zygoptera and three Anisoptera species were recorded at waterbodies, which could not be recorded at meadow sites. Hence, only five out of eleven Zygoptera species recorded at waterbody sites were found at meadow sites. Accordingly, 15 out of 18 Anisoptera species recorded at waterbody sites were also observed at meadow sites (Table 2).

The most frequent Odonata species at surveyed meadow sites was *Platycnemis pennipes* (231 individuals; 35% of counted total at meadow sites), followed by *Aeshna isoceles* (127; 19%), *Aeshna mixta* (67; 10%) and *Orthetrum cancellatum* (40; 6%). Anisoptera species (62% of all individuals recorded at meadow sites) were more abundant on meadows than Zygoptera (38% of individuals). At waterbody sites, zygopterans were more abundant than anisopterans (Figure 2).

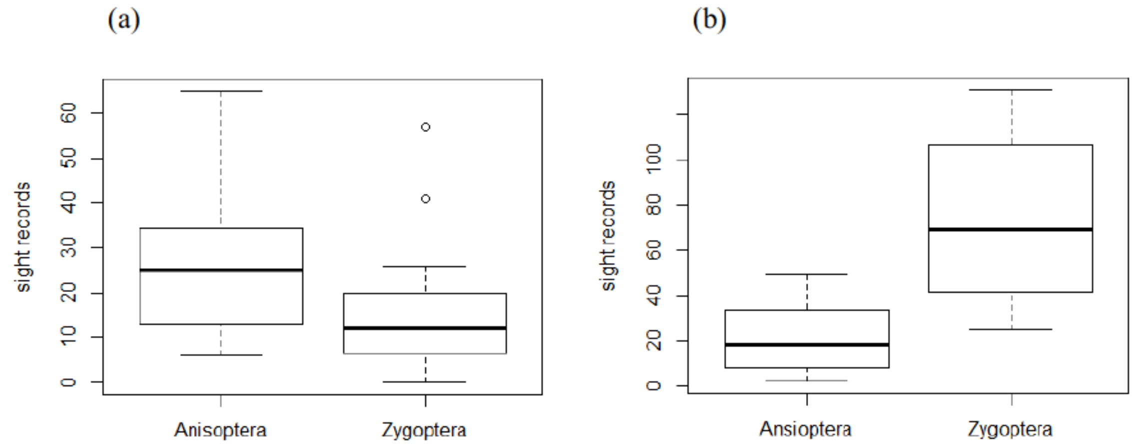

Figure 2: Median number of individuals counted per transect ± IQR (box) and 1.5 * IQR (whiskers) of Anisoptera and Zygoptera (a) at meadow sites and (b) at waterbody sites.

Table 2. Number of individuals recorded per sampling site over entire sampling period.

Suborder Zygoptera	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	M15	M16	W1	W2	W3	W4	W5	W6	W7	W8
Family Calopterygidae																								
Calopteryx splendens (Harris, 1782)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	7	1	0	0	0	0
Family Lestidae																								
Lestes viridis (Vander Linden, 1825)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0
Lestes sponsa (Hansemann, 1823)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sympecma fusca (Vander Linden, 1820)	0	0	0	0	2	0	2	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Family Coenagrionidae																								
Coenagrion hastulatum (Charpentier, 1825)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Coenagrion puella (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	19	10	16	64	8
Erythromma najas (Hansemann, 1823)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	5	4	0	16
Erythromma viridulum (Charpentier, 1840)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	7	0	0	10
Ischnura elegans (Vander Linden, 1820)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	2	6	6	32	19	0	0
Ischnura pumilio (Charpentier, 1825)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
Family Platycnemididae																								
Platycnemis pennipes (Burmeister, 1839)	6	16	13	0	2	9	1	5	10	23	41	12	11	13	23	46	20	117	57	39	59	10	4	0

Suborder Anisoptera	**M1**	**M2**	**M3**	**M4**	**M5**	**M6**	**M7**	**M8**	**M9**	**M10**	**M11**	**M12**	**M13**	**M14**	**M15**	**M16**	**W1**	**W2**	**W3**	**W4**	**W5**	**W6**	**W7**	**W8**
Family Gomphidae																								
Gomphus vulgatissimus (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	1	0	0	0
Family Aeshnidae																								
Aeshna affinis (Vander Linden, 1820)	0	0	0	5	2	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	1	1
Aeshna cyanea (Müller, 1764)	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0
Aeshna grandis (Linnaeus, 1758)	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aeshna isoceles (Müller, 1767)	1	1	12	41	13	1	6	3	7	1	0	15	25	0	0	1	0	0	0	2	0	1	0	2
Aeshna mixta (Latreille, 1805)	0	1	11	4	1	0	1	1	1	0	3	13	28	2	1	0	0	0	0	1	1	0	0	4
Anax imperator (Leach, 1815)	1	4	5	2	4	2	2	4	2	1	1	3	0	3	2	2	1	0	0	4	4	1	0	2
Anax parthenope (Selys, 1883)	0	0	0	0	0	1	0	0	0	0	2	0	0	0	1	0	1	0	0	0	0	0	0	0
Brachytron pratense (Müller, 1764)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Family Corduliidae																								
Somatochlora metallica (Vander Linden, 1825)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	2

Suborder Anisoptera (continued)	**M1**	**M2**	**M3**	**M4**	**M5**	**M6**	**M7**	**M8**	**M9**	**M10**	**M11**	**M12**	**M13**	**M14**	**M15**	**M16**	**W1**	**W2**	**W3**	**W4**	**W5**	**W6**	**W7**	**W8**
Family Libellulidae																								
Crocothemis erythraea (Brullé, 1832)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	0	0	0
Libellula depressa (Linnaeus, 1758)	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Libellula quadrimaculata (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Orthetrum albistylum (Selys, 1841)	0	0	0	0	3	0	1	0	0	1	0	0	0	1	0	4	0	0	0	0	0	0	0	0
Orthetrum cancellatum (Linnaeus, 1758)	3	2	6	2	0	0	0	4	7	0	1	2	6	1	3	3	5	0	0	8	25	9	0	0
Sympetrum sanguineum (Müller, 1764)	8	0	0	0	0	0	1	2	6	0	2	0	0	4	1	12	1	0	0	14	3	2	1	5
Sympetrum striolatum (Charpentier, 1840)	3	1	1	0	1	2	1	4	2	2	0	1	3	1	2	4	0	1	0	0	6	4	2	0
Sympetrum vulgatum (Linnaeus, 1758)	7	4	0	0	3	0	0	2	2	3	2	1	0	0	9	6	2	2	2	4	5	6	12	4
	30	**31**	**48**	**55**	**29**	**15**	**15**	**31**	**37**	**31**	**53**	**47**	**76**	**25**	**42**	**80**	**37**	**135**	**72**	**133**	**169**	**76**	**84**	**54**

Species richness

Figure 3 shows species accumulation curves, calculated for meadow sites and waterbody sites. Additionally, a species accumulation curve using a pooled dataset that combines records of meadows and waterbody sites was calculated. Recorded species richness was higher at waterbodies than on meadows. However, the extrapolated part of the curve for the Odonata assemblage on meadows indicates similar species richness of both habitat types.

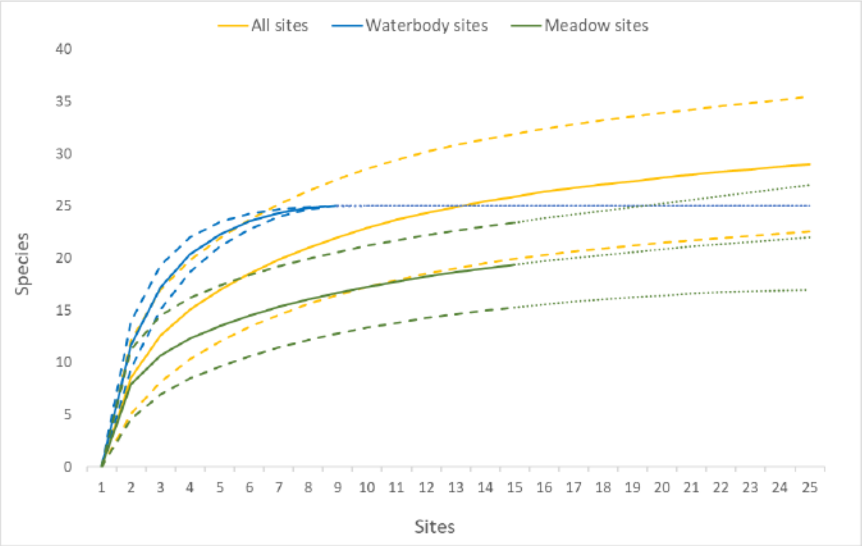

Figure 3: Species-accumulation curves (± 95% CI) calculated for all sites, waterbody sites and meadow sites. Dotted lines represent extrapolated values.

While no correlation between species richness and distance to nearest waterbodies could be found when testing for all recorded species (r = -0.36, p = 0.16), Zygoptera species richness declined significantly with increasing distance to waterbodies (r = -0.56, p = 0.02). In contrast, no significant relationship was found between Anisoptera species richness and distance to waterbodies (r = -0.19, p = 0.46). Species richness was not significantly influenced by structural diversity of the forest margin (SDIa) when tested for all recorded species (ANOVA: $F_{1,16} = 0.006$, p = 0.94). However, Pearson's product-moment correlation shows that overall species richness is significantly associated with SDIb (r = 0.61, p = 0.01) (Figure 4). If taxonomical groups are considered individually, species richness of Anisoptera showed a strong positive correlation with SDIb (r = 0.69, p = 0.002), species richness of Zygoptera on the other hand was not significantly influenced by SDIb (r = 0.26, p = 0.31).

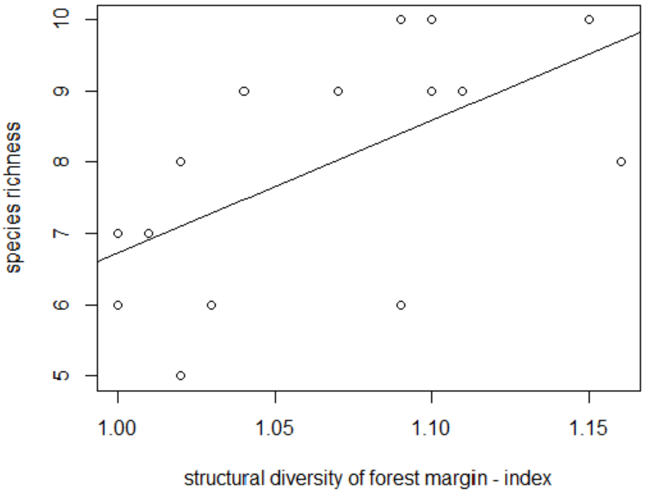

Figure 4. Species richness in relation to calculated structural diversity index of forest margin (SDIb).

Abundance

While no significant correlation between the total number of recorded individuals and the distance to the closest waterbody could be observed (r = 1.14, p = 0.62), models that test Anisoptera and Zygoptera separately, yielded highly significant results. Anisoptera counts increased significantly with increasing distance to waterbody (r = 0.50, p = 0.05), by contrast, counted individuals of the suborder Zygoptera showed a highly significant negative correlation with increasing distance from a waterbody (r = -0.65, p = 0.006; Figure 5).

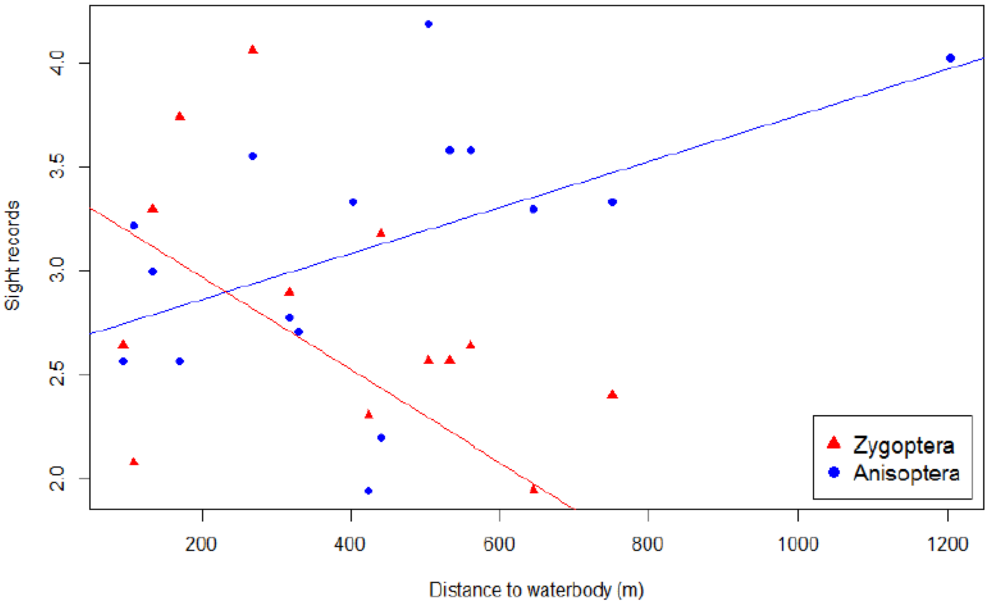

Figure 5: Relationship between recorded number of individuals (log-transformed) and distance to closest waterbody.

A comparison of relative abundances of Zygoptera and Anisoptera specimens recorded at meadow and waterbody sites (Figure 6) illustrates that Anisoptera species were more abundant on meadows than Zygoptera. In comparison, Zygoptera were more dominant at waterbodies. Notably, *Platycnemis pennipes* was equally distributed on meadows and waterbodies.

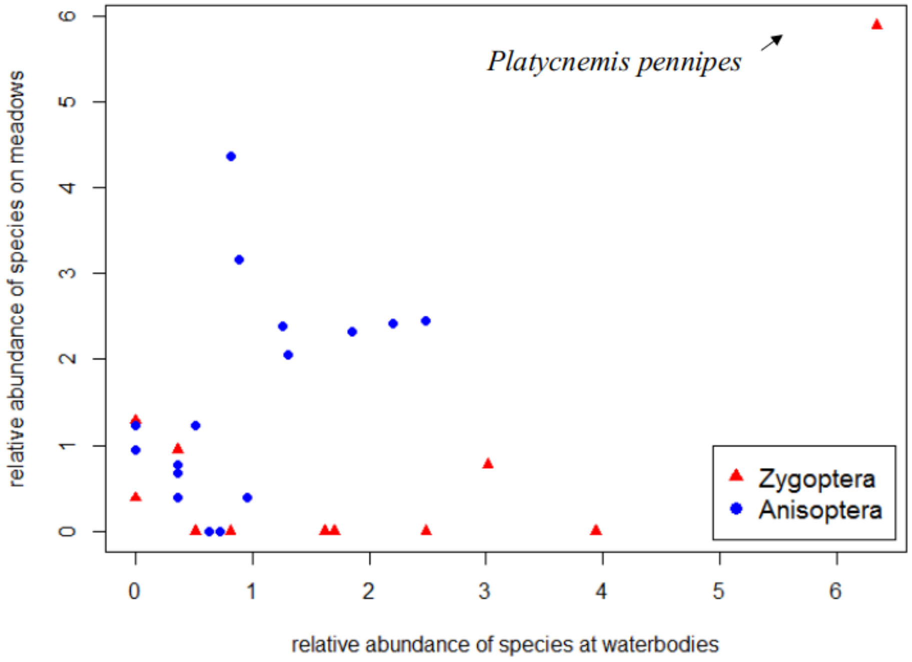

Figure 6. Relative abundance of Anisoptera and Zygoptera occurring at waterbody and meadow sites.

Effects of several habitat variables on the abundance of dragonflies were tested. A Kruskal-Wallis rank sum test shows that the number of individuals (H = 6.41, p = 0.04) can be significantly associated with structural diversity of the forest margin (SDIa). A post-hoc Kruskal-Nemenyi test shows that the mean number of dragonfly records at habitats with intermediate and highest structural diversity differ significantly (H = 3.40, p = 0.04; Figure 7). Testing for effects of structural diversity (SDIa) on the occurrence of zygopterans and anisopterans separately, showed that occurrence of Anisoptera species was significantly influenced by the structural diversity of the forest margin (H = 6.22, p = 0.04), however no significant results could be found for Zygoptera species (H = 0.54, p = 0.75). Moreover, no significant correlation between calculated structural diversity index of forest margin (SDIb) and species counts could be found (r = 0.27, p = 0.30). Also, the height of the herb layer was not significantly related to dragonfly abundance (r_s = 0.05, p = 0.55).

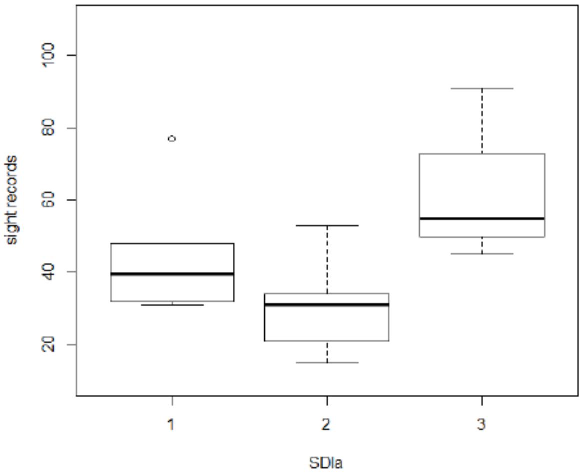

Figure 7. Median number of Odonata individuals ± IQR (box) and 1.5 * IQR (whiskers) on meadows with different structural diversity (SDIa) of the adjacent forest margin ranging from 1-3.

Species composition

The NMDS ordination based on Bray-Curtis similarities (Figure 8) shows that species composition of sites can be grouped according to their distance from a waterbody. Sites located at greatest distance from a waterbody (indicated by grey-colored dots) show a similar pattern in species composition and form a distinct group. Communities of sites with intermediate distance from a waterbody (indicated by white dots) are slightly interspersed with sites of lowest distance to waterbody (indicated by black dots). The stress value of the NMDS ordination model indicates that it is reliable in visualizing the similarity relationships between sampled meadows.

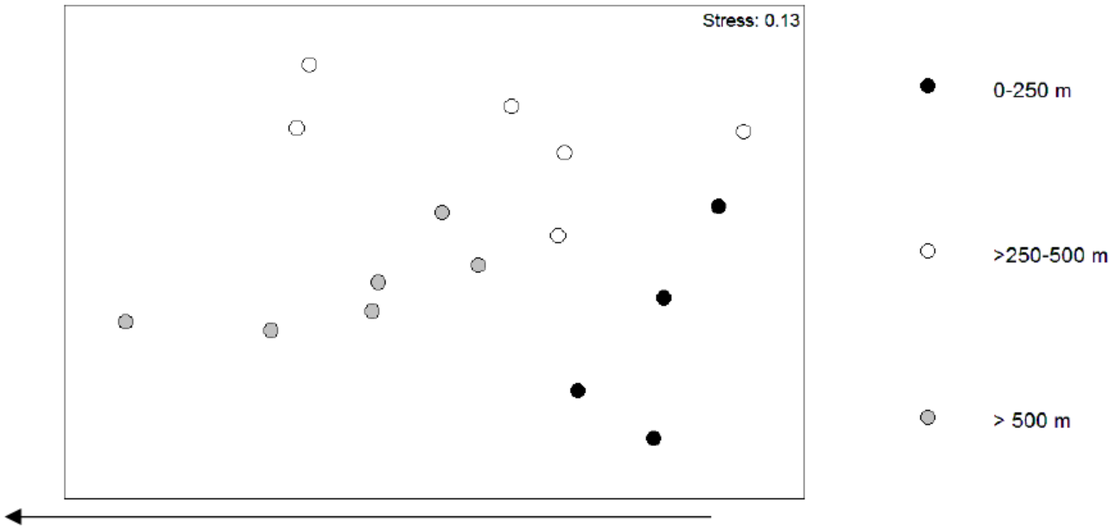

Figure 8. NMDS ordination of meadow sites based on Bray-Curtis similarities. Black points represent sites with a distance to the closest waterbody between 0-250 m, white dots represent waterbody distance of >250-500 and grey dots represent sites with waterbody distance of >500 m. Stress: 0.13.

Dimension 1 values of the NMDS ordination visualizing similarity relationships of species assemblages on meadows were significantly related the distance to waterbodies (r = -0.71, p = 0.002).

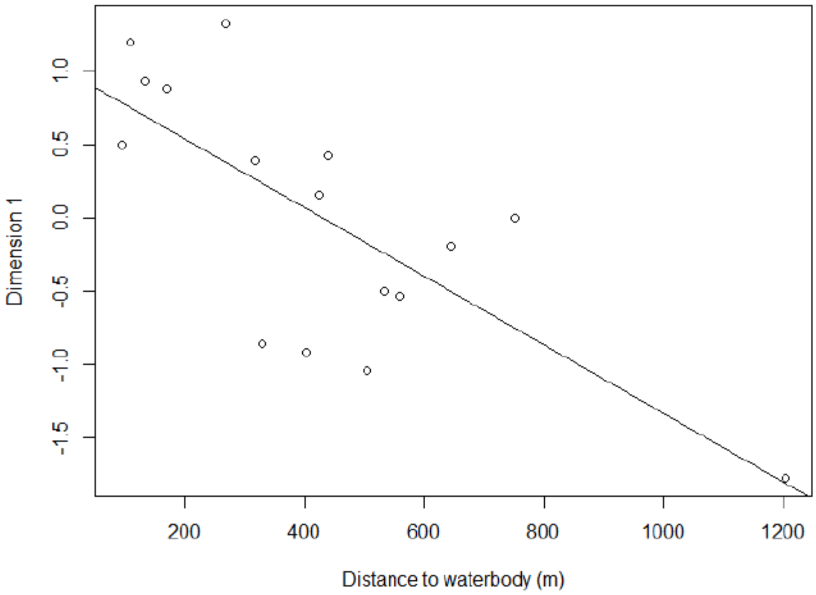

Figure 9. Relationship between similarity in species composition (Dimension 1 values extracted from NMDS ordination based on Bray-Curtis similarities for Odonata assemblages recorded on meadows; compare Figure 8) and distance to waterbodies.

A one-way ANOSIM showed that species composition differs significantly between categories of distances to waterbodies (0-250 m, > 250-500 m, >500 m) (r_{global} = 0.49, p = 0.001; Table 3). Pairwise comparisons illustrate a highly significant difference between all distance groups (Table 4).

It was tested whether structural diversity of habitats (SDIa) influences species composition. A one-way ANOSIM shows that species composition differs significantly between categories of structural diversity (r_{global} = 0.27, p = 0.009). While pairwise comparisons revealed that sites showing high diversity and intermediate diversity each differ significantly from structurally less diverse sites, a pairwise test between diversity classes SDIa 2 and SDIa 3 did not yield a significant result (Table 5). Moreover, a one-way ANOSIM showed that sites located south and north of the levee did not differ significantly in community structure. Also, no significant correlation between the structure of dragonfly assemblages and the structural diversity index (SDIb) could be found (r_s = 0.37, p = 0.15).

Table 3. Results of one-way ANOSIMs (max. number of allowed permutations 999; based on Bray-Curtis similarity index) testing for effects of distance to waterbodies, structural diversity of meadows and their location on Odonata species composition.

Species composition	r_{global}	p
Distance to waterbody	0.49	0.001
Structural diversity index	0.27	0.009
Location (south/north/levee)	0.16	0.590

Table 4. Results of pairwise comparisons (ANOSIM) testing for effects of distance of meadows to waterbodies on Odonata species composition.

Pairwise comparisons	r_{global}	P
0-250 m vs. >250-500 m	0.67	0.005
0-250 m vs. > 500 m	0.69	0.005
>250-500 m vs. > 500 m	0.27	0.006

Table 5. Results of pairwise comparisons of (ANOSIM) testing for effects of SDIa (Structural diversity index) on Odonata species composition.

Pairwise comparisons	r_{global}	p
1 vs. 3	0.42	0.03
1 vs. 2	0.24	0.01
3 vs. 2	0.19	0.18

Sex-specific differences in spatial distribution

Only a subset of species allowed identification of the sex in the field. A list of species that were included in the following calculations can be found in the appendix A5. Male dragonflies (75%) were generally more dominant in the study area than females (25%). A comparison of relative abundances of males and females shows that male Odonata were generally more dominant on meadows than females (Figure 10a). With respect to waterbody sites, 88% of recorded Odonata were males and 11% females (Figure 10b), resulting in a male-biased sex ratio at both types of sampling sites. The recorded sex ratio at meadows was 2.3:1, the sex ratio at waterbodies was 10:1.

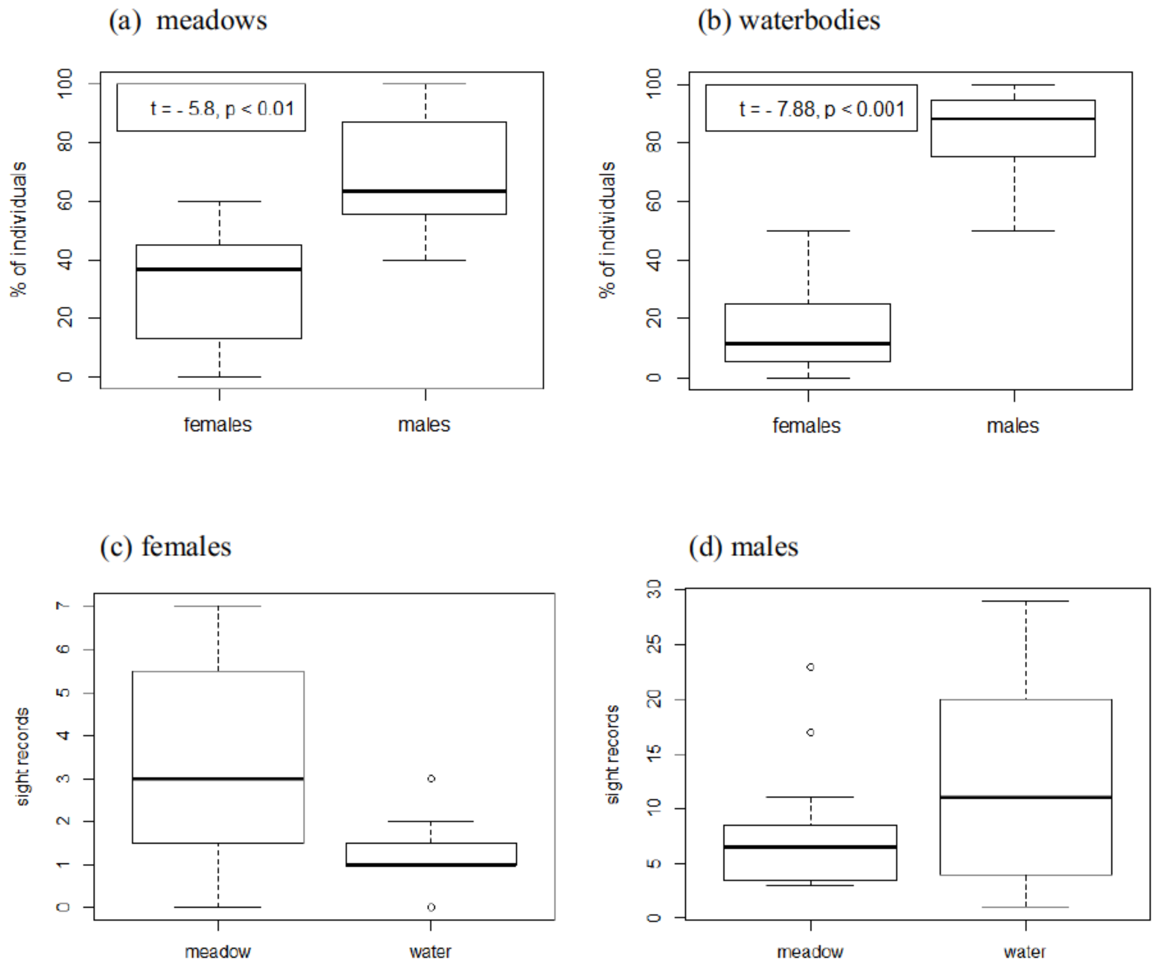

Figure 10. Sex-specific differences in relative and absolute abundance at sampling sites: (a) relative abundance of female (median = 36%) and male Odonata (median = 63%) on meadows; (b) relative representation of female (median = 11%) and male (median = 88%) Odonata at waterbody sites; (c) abundance of female dragonflies on meadows (mean = 3.25) and waterbodies (mean = 1.25); (d) abundance of male dragonflies on meadows (7.6) and waterbodies (12.5). Calculation includes subset of dragonflies that allowed sex identification. All medians are shown with ± IQR (box) and 1,5 * IQR (whiskers).

Prey availability

Prey abundance ranged from 0 to 1000 estimated flying insects (*median* = 20) per visit. After removal of outliers (200, 500 and 1000), Spearman's rank correlation revealed a strongly significant correlation between the number of recorded dragonflies and damselflies and prey abundance ($r_s = 0.26, p < 0.001$) for all sites. However, if only meadow sites were included in the model, no significant correlation between those variables could be detected ($r_s = 0.12, p = 0.20$). Spearman's rank correlation shows a highly significant correlation between prey abundance recorded at waterbodies and abundance of Odonata at waterbodies ($r_s = 0.58, p < 0.001$).

Species-specific distances and distribution of species

Maps visualize the spatial distribution of some Odonata species across our sampling sites to illustrate species-specific differences in utilizing meadows as foraging habitats. Figure 11 shows Odonata species that occurred on sampled meadows, arranged according to the farthest distance the species was observed from a waterbody. Anisopterans were recorded on meadows up to 1205 meters away from waterbodies, zygopterans were recorded up to 750 meters away from waterbodies.

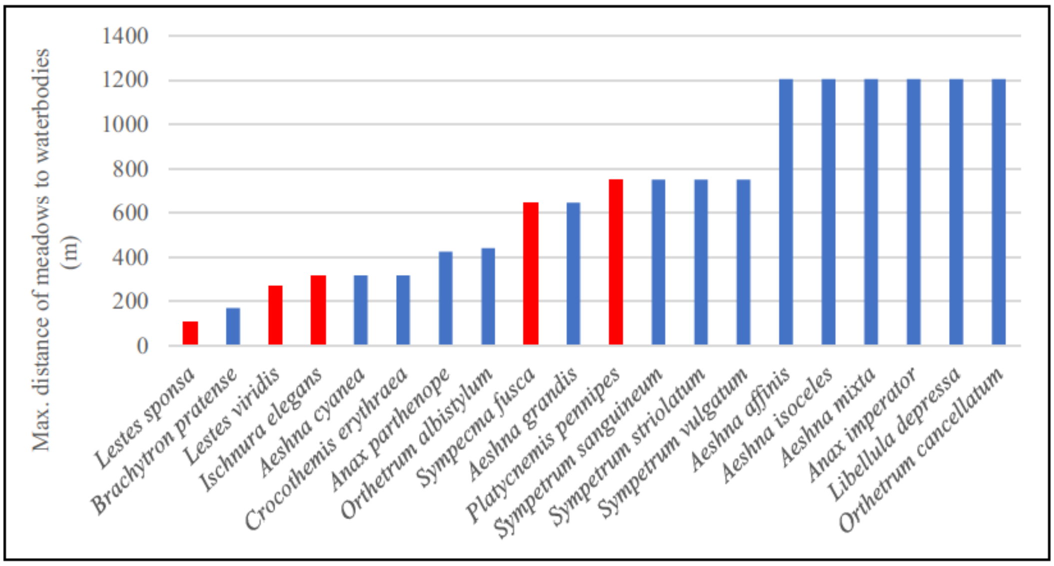

Figure 11. Odonate species observed on meadows, arranged according to the farthest distance Odonata species were observed from waterbodies. The figure includes species that were present on meadows. Red bars represent Zygoptera species, blue bars represent Anisoptera species.

Common species

Platycnemis pennipes was the most abundant species in the study area. This species occurred on meadows in a distance of up to 750 meters from nearest waterbodies and was widely distributed in the study area (Figure 12). Although *Platycnemis pennipes* was also found on most meadows, a negative trend between its abundance and distance to waterbodies could be found (r = -0.44, p = 0.08). *Platycnemis pennipes* showed strikingly high abundances at waterbody sites located at Kleine Binn (sites W2, W3 and W4).

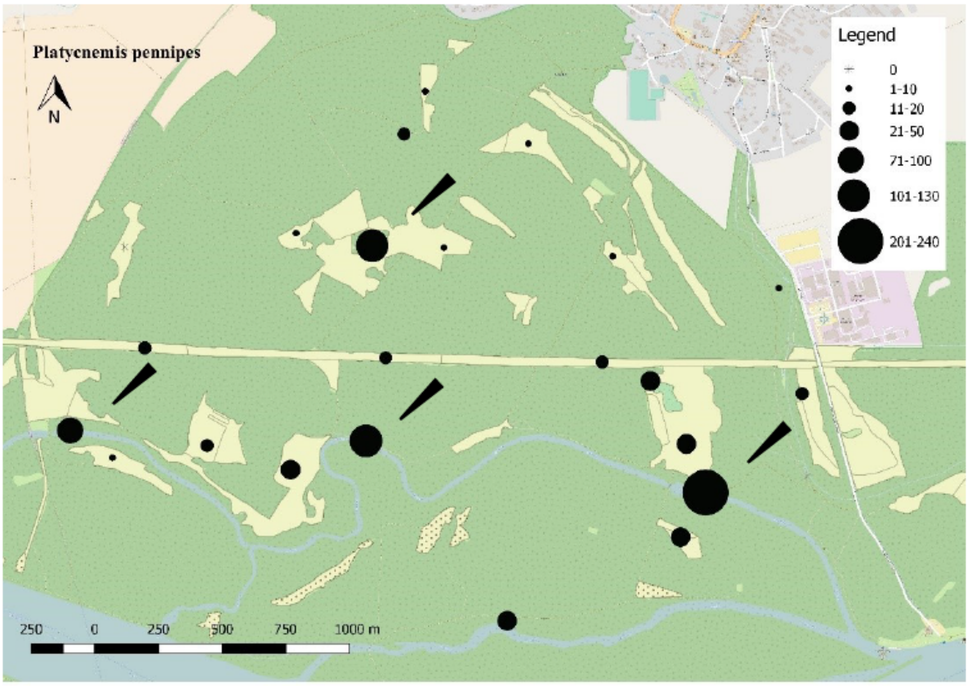

Figure 12. Abundance of *Platycnemis pennipes* at sampled study sites. Black arrows indicate sites with particularly high abundances.

Aeshna isoceles was highly abundant on the Marchfeld levee and was recorded at meadows in distances of up to 1205 meters from waterbodies (Figure 13). However, this species was generally widely distributed in the study area.

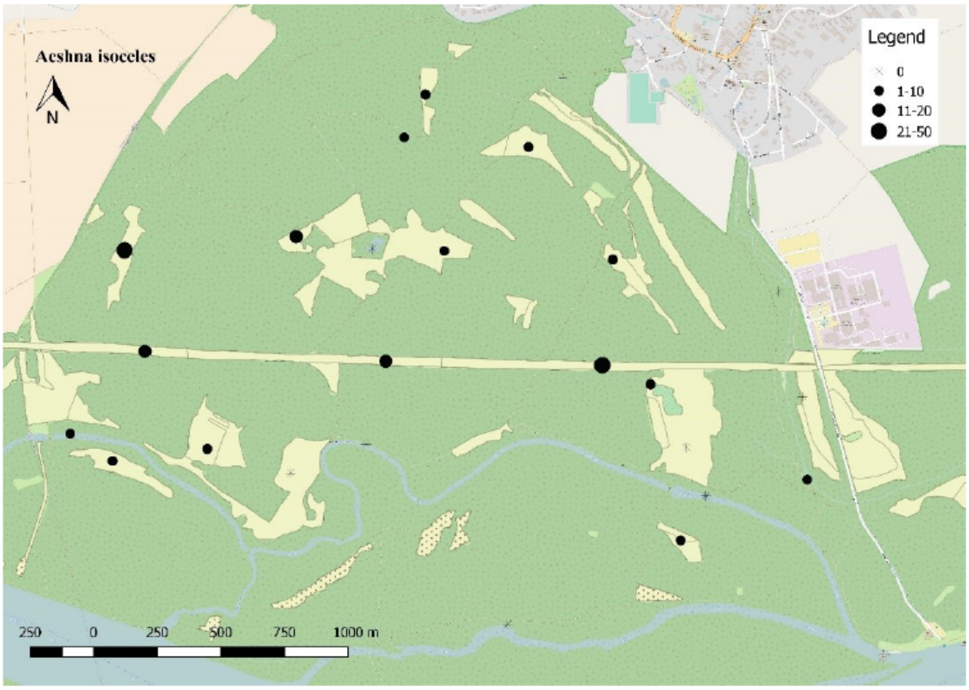

Figure 13. Abundance of *Aeshna isoceles* at sampled study sites.

Species with localized occurrence

Ischnura elegans was observed at both, lotic and lentic waterbodies. This species was only observed at meadows located near (≤ 315m) to waterbodies. However, this result has to be considered with caution, as only a total of four individuals were observed on meadows.

Figure 14. Abundance of *Ischnura elegans* at sampled study sites. Black arrows indicate sites with particularly high abundances.

Coenagrion puella was exclusively observed at waterbodies and was very abundant at sites with lush aquatic vegetation or along slow-flowing waterbodies.

Figure 15. Abundance of *Coenagrion puella* at sampled study sites. Black arrows indicate sites with particularly high abundances.

Species highly abundant on Marchfeld levee

Aeshna mixta was also highly abundant on the Marchfeld levee and occurred on meadows in distances of up to 1205 meters to waterbodies.

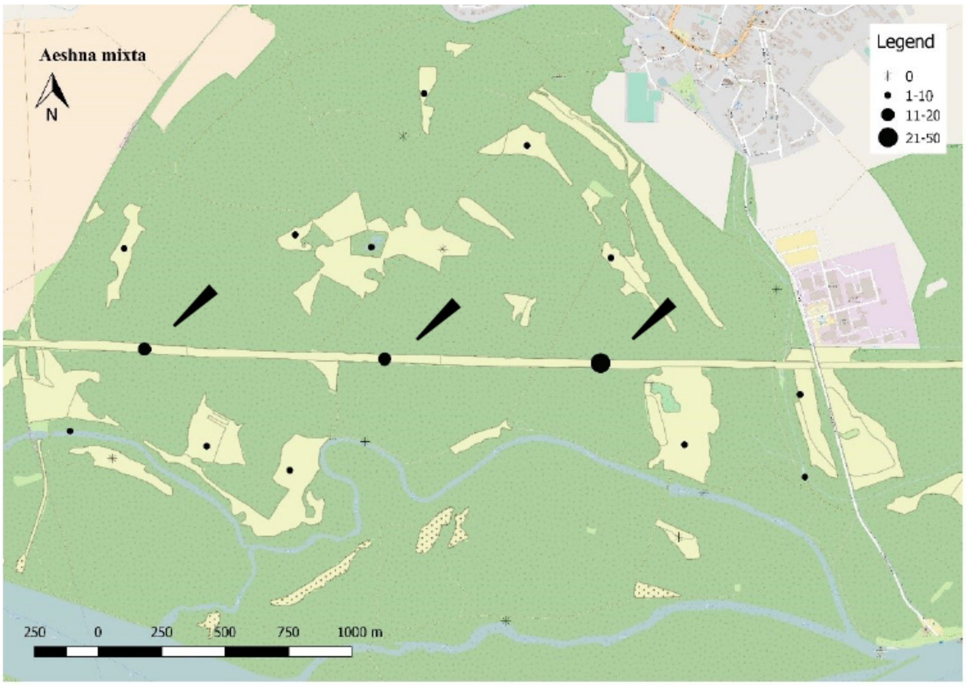

Figure 16. Abundance of *Aeshna mixta* at sampled study sites. Black arrows indicate sites with particularly high abundances.

Comparison of members of the genus Sympetrum

Sympetrum sanguineum was generally widely distributed in the study area, however, it was not observed on the Marchfeld levee (Figure 17). *Sympetrum vulgatum* was only recorded once on the levee and was otherwise evenly distributed in the study area (Figure 19). In comparison, *Sympetrum striolatum* also occurred on the levee (Figure 18).

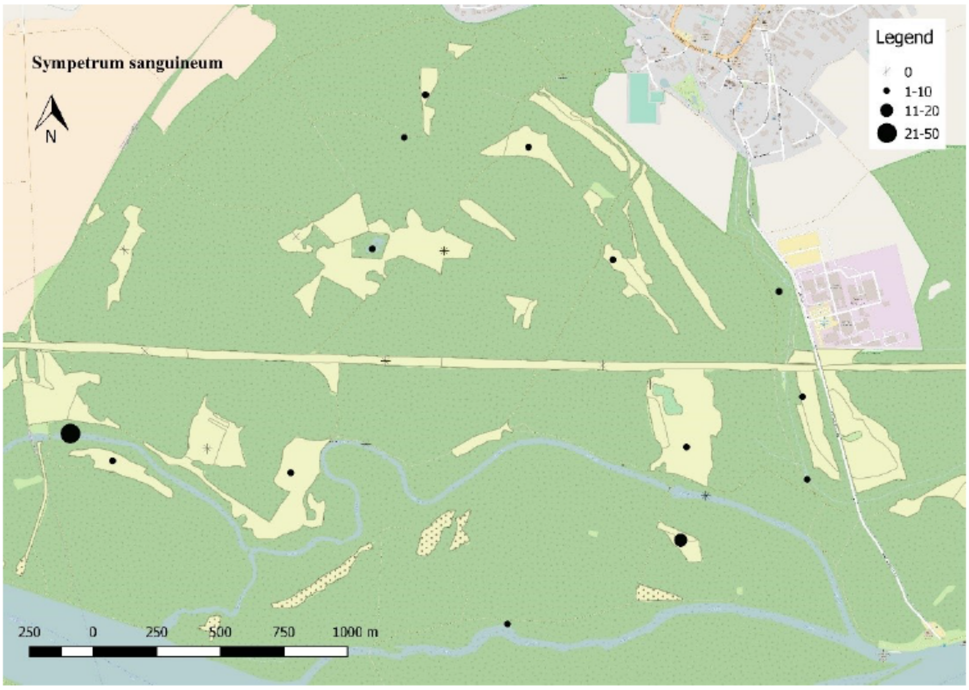

Figure 17. Abundance of *Sympetrum sanguineum* at sampled study sites.

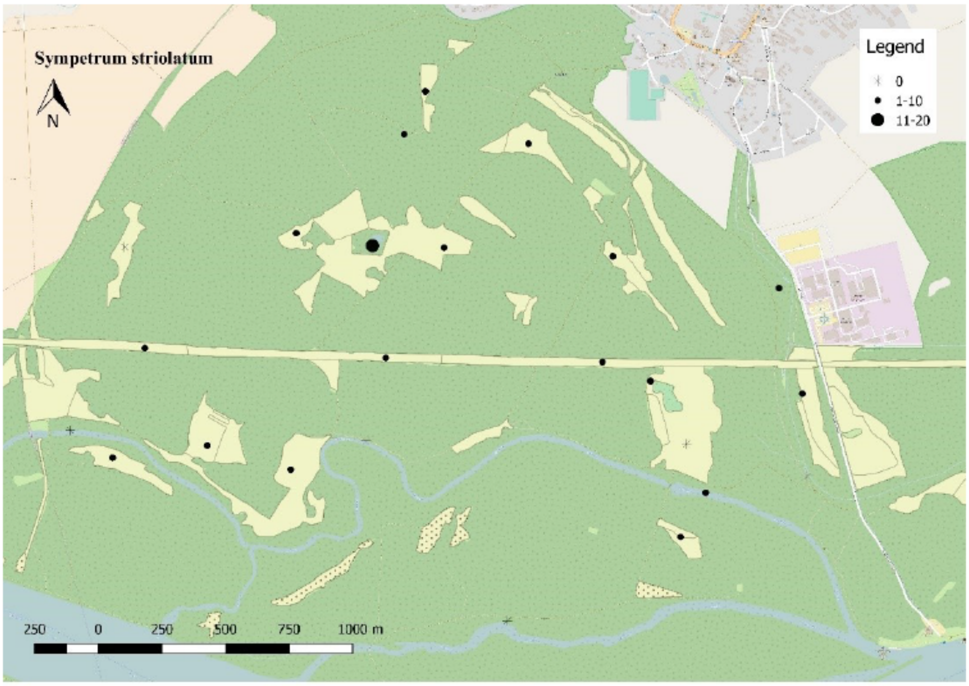

Figure 18. Abundance of *Sympetrum striolatum* at sampled study sites.

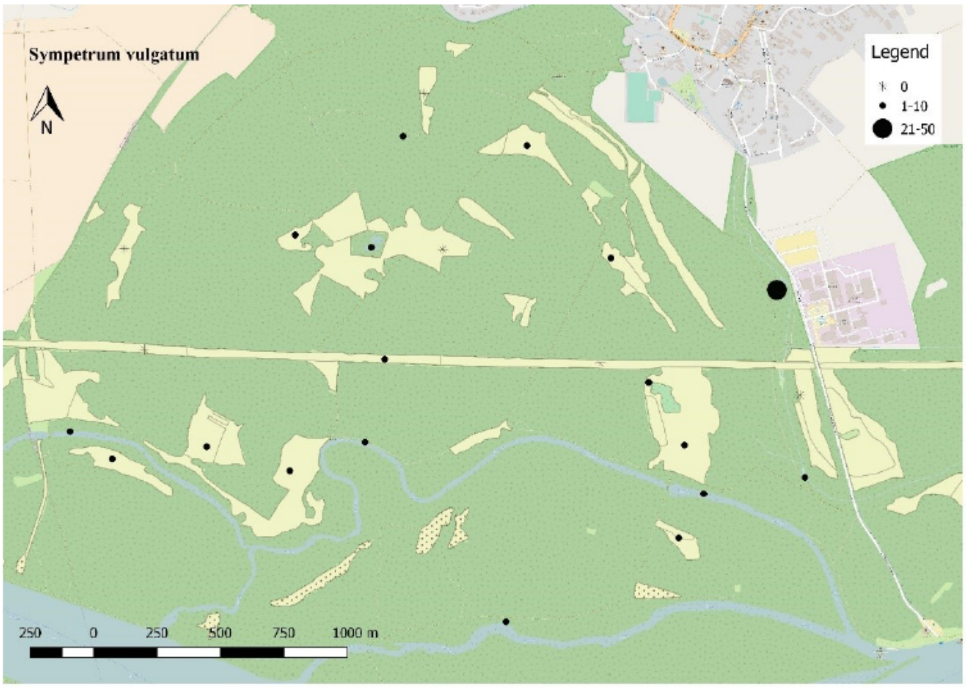

Figure 19. Abundance of *Sympetrum vulgatum* at sampled study sites.

Discussion

Odonata species observed in this study represent 88% of the dragonfly and damselfly fauna recorded for the study area at Orth an der Donau (Raab, 2000) and 38% of Austria's Odonata fauna (Raab, 2006).

Anisopterans were generally more abundant on meadows than zygopterans. A total of 62% of all individuals recorded at meadow sites were anisopterans, 38% zygopterans. However, this percentage is highly influenced by the proportion of *Platycnemis pennipes*, a species widely distributed over the entire study area. *Platycnemis pennipes* was quite evenly distributed on sampled meadows and waterbodies. With regard to the distribution of Zygoptera and Anisoptera in the study area, the opposite was true at waterbody sites, zygopterans outnumbered anisopterans significantly.

Species richness

Species accumulation curves reveal that species richness was slightly higher at waterbodies than on meadows. Few zygopterans observed at waterbodies occurred on sampled meadows. In fact, only three Zygoptera species observed at waterbodies could be found on meadows. With the exception of *Ischnura elegans*, none of the Zygoptera species belonging to the family Coenagrionidae recorded at waterbodies were observed on meadows. Also, the rheophilic species *Calopterix splendens* and *Gomphus vulgatissimus* (Dijkstra, 2014) were present at sampled waterbodies but could not be recorded on meadows. Concerning anisopterans, 15 species observed at waterbodies were found on meadows. Although some species recorded at meadow sites could not be observed at waterbodies (*Lestes viridis*, *Lestes sponsa* and *Aeshna grandis*), species richness at sampled waterbodies was still higher than on meadows. Zygoptera species richness declined with increasing distance from waterbodies. Given the assumption that zygopterans generally display poorer flight ability than anisopterans (Corbet, 1999), it is not surprising that fewer dragonfly species of the suborder Zygoptera were found on meadows. Moreover, also intraguild predation risk may come into place, preventing zygopterans from foraging in habitats where anisopterans are abundant (Corbet, 1999).

Other than expected, no relationship between structural diversity of forest margins and species richness could be found, however the significant correlation detected between heterogeneity of forest margin structure reflected in SDIb and species richness suggests that increased species richness can be expected if structural diversity of forest margins is high. This assumption is applicable for anisopterans, albeit, no such relationship could be found for zygopterans.

Sex-specific dispersal patterns

It is generally assumed that males and females differ in their tendency to disperse. Various authors describe that sex ratios at reproductive sites are mostly male-biased, once sexual maturity has been reached. Males spend most of their time at breeding sites awaiting females, females on the other hand visit reproductive sites predominantly to mate and oviposit, suggesting that they spend a great deal of time away from waterbodies and are more likely to disperse (Conrad, et al., 1999; Corbet, 1999; Suhonen, et al., 2008; Utzeri, et al., 1988). Various capture-mark-recapture studies confirm male-biased sex ratios at waterbodies (McCauley, 2006), sustaining the hypotheses that males are more abundant at breeding sites than females, the opposite can therefore be assumed true on meadows. Our study found that male-biased sex ratios exist at both, waterbody sites and meadow sites, however, the sex ratio at waterbodies was substantially more biased towards males than on meadows. Patterns in sex ratio at waterbodies can be the result of intraspecific faunal interactions. At breeding sites with high male density, females were reported to move away from waterbodies in an attempt to avoid excessive matings or harassment of males (Suhonen, et al., 2008). In territorial dragonflies with male density at reproductive sites assumed rather low, females may benefit in that harassment during copulation or oviposition is reduced. Also, predation risk may be reduced in high-quality territories, hence areas were territorial males are present (Suhonen, et al., 2008). Higher abundances of females in such territories are a logical consequence. A study that investigated dispersal ability of *Coenagrion puella, Coenagrion scitulum* and *Libellula depressa* demonstrated that females show higher dispersal tendencies than males. This tendency was particularly ascribed to territorial behaviour of *L. depressa* males (Angelibert & Giani, 2003).

Other than expected, female abundance was not associated with distance from a waterbody. It was hypothesized that female abundance would increase with increasing distance from a waterbody, however no such relationship was observed. Similarly, Hykel and others (2016) weren’t able to detect a significant difference between the abundance of males and females in relation to the effect of distance from their natal site.

Territorial behavior at foraging sites may also influence distribution of the sexes. While conspecifics are normally described to forage together without showing aggressive behavior and are often mingled together in foraging aggregations, some studies reported aggressive interactions between conspecifics (e.g. *Sympetrum)*, dragonflies defending foraging perches. Interestingly, a study investigating *Sympetrum sanguineum,* demonstrated that females showed stronger aggressive behavior when defending a foraging perch against males than conspecific females (Corbet, 1999).

Abundance

Our results suggest that dispersal is strongly associated with Odonata suborder. Anisoptera records increased significantly with increasing distance from a waterbody. The opposite could be confirmed for zygopterans, which were present in great abundance, if meadows were located in close vicinity to a waterbody and decreased steeply with increasing distance from waterbodies. If distances moved by single species are considered, only few zygopterans moved long distances from meadows. With the exception of *Platycnemis pennipes* (recorded on meadows in distances of up to 750 meters from waterbodies) and *Sympecma fusca* (up to 645 meters from waterbodies), none of the Zygoptera species dispersed more than 350 meters. Anisoptera species on the other hand were recorded on meadows up to 1205 meters away from waterbodies. With the exception of *Aeshna cyanea* and *Anax parthenope*, all species that belong to the taxonomical group Aeshnidae, were found more than 600 meters away from waterbodies. With regard to the family Libellulidae, *Libellula depressa* and *Orthetrum cancellatum* were observed one kilometer away from waterbodies. All species of the genus *Sympetrum* were observed on meadows up to 750 meters away from waterbodies. In short, distance from a waterbody and abundance of zygopterans and anisopterans showed different relationships. This corresponds with findings obtained through capture-mark-recapture studies stating that dispersal probability generally appears to increase with species size and larger species being more likely to disperse greater distances (Conrad, et al., 1999). With regard to the species recorded in the study area, larger species generally moved longer distances than smaller species.

Quality of vegetation, such as structure or density are generally assumed to influence abundance of dragonflies (Buchwald, 1992; Foote, 2005; Hykel, et al., 2016; Sternberg & Buchwald, 2000; Wildermuth, 2012). Although most existing research concentrated on investigating the influence of riparian vegetation in immediate vicinity of waterbodies

(Buchwald, 1989; Wildermuth, 1994), the results of this study suggest that heterogeneity of vegetation structure in terrestrial habitats is of major importance for dragonflies and damselflies. High structural diversity of forest margins was significantly associated with occurrence of dragonflies. Differences in dragonfly abundance was most significant between habitats with intermediate and highest structural diversity. Interestingly, dragonflies were slightly more abundant on meadows with low heterogeneity of vegetation structure than intermediate, however the difference was not significant. High abundances of *Orthetrum cancellatum* on the Marchfeld levee may have led to that result. Sampling sites on the levee were all classified uniform in terms of forest margin diversity because big trees characterize the landscape. *Orthetrum cancellatum* is not as dependent of perching or refuge opportunities in shrubs as other species and uses stony trails for resting between flights (Dijkstra, 2014).

Unlike zygopterans, anisopterans responded positively to heterogeneously structured vegetation in forest margins. Thus, vegetation structure does not only seem to be associated with species richness but also with Odonata abundance. However, this result has to be considered with caution, because only few zygopterans occurred on meadows. It is expected that zygopterans more likely use riparian vegetation growing along water banks for pairing or copulation (Hykel, et al., 2016).

While it was hypothesized, that dragonflies would be more abundant if the mean height of herb layer was high, no such relationship could be observed within this study. A similar result was found in a study on *Sympetrum depressiusculum.* This study demonstrated that cover of tall vegetation instead of height thereof and vegetation cover in general would more likely have an effect on overall dragonfly occurrence (Hykel, et al., 2016), thus presence of fairly tall vegetation seems more relevant than height. Moreover, not all species demand tall vegetation and rather seek refuge in trees or shrubs of forest margins (Dijkstra, 2014). However, the importance of vegetation height for Odonate's choice of roosting refuge should not be neglected. A study found that zygopterans, in average, roosted at heights of around 50 centimeters, suggesting that a certain minimum in height for roosting perches is favored (Rouquette & Thompson, 2007). Additionally, anecdotal observations revealed that various species (e.g. *Libellulidae*) used dried reed beds embedded in forest margins for perching. Recording such structural traits could bring more insight into its relevance on abundance of certain species on meadows in future studies.

A limiting factor for the occurrence of dragonflies and damselflies may be prey abundance. Adult Odonata forage more frequently where availability of potential prey is high (Corbet, 1999; Kirkton & Schultz, 2001). Hykel et al. (2016) reported that abundance of arthropods was significantly associated with the abundance of dragonflies and damselflies. Our results found a similar relationship, however, this was only true for pooled data including waterbody sites, but did not reach significance if tested for meadow sites only.

Species composition

This study demonstrated that species composition on meadows was strongly affected by the distance from waterbodies. We classified meadows in terms of distance from a waterbody and found that meadow sites with similar distance characteristics were similar in species assemblage composition. These results do not only reflect differences in dispersal behavior between zygopterans and anisopterans, but also exhibit species-specific dispersal properties within suborder and family, elucidated further under section ‘Species-specific distances’.

Community structure may be shaped by faunal interactions such as interspecific competition. Interspecific aggression may force individuals of subdominant species to move to other, less preferred habitats (Tynkkynen, et al., 2008) or even lead to the exclusion of some species from certain waterbodies (Moore, 1964). Whereas such aggressive interactions have mainly been described at reproductive sites (Moore, 1964; Suhonen, et al., 2008), interspecific competition is also assumed to play a prominent role in terrestrial habitats (Corbet, 1999). Whereas different odonate species such as aeshnids have been reported to forage together at foraging sites without evident interaction, in some cases showing vertically or horizontally (Corbet, 1999; Kennedy, 1917; Perry, et al., 1977) stratified patterns, observations obtained through this study and reported by other researchers (Moore, 1991) showed that some species often display aggressive behavior towards other species at foraging sites. Observational findings obtained through this study showed that some larger species (e.g. *Anax imperator)* frequently chased off other dragonflies during foraging flights, suggesting that dragonflies also display territorial behavior at foraging sites.

Structural characteristics of forest margins also seem to shape community structure on meadows. Composition of dragonfly assemblages on meadows with intermediate and high heterogeneity differed from meadows with uniform forest margin structure, potentially reflecting species with varying demands on vegetation structure at terrestrial habitats. Whereas habitat generalists and specialists have been described in terms of reproductive habitat requirements (Raab, 2006), knowledge on the demands of Odonata on vegetation structure at terrestrial habitats is limited. Other than expected, species composition north and south of the levee did not differ significantly.

Species-specific distances

Platycnemis pennipes was the most abundant dragonfly species in the study area. This species is characteristic in floodplain systems and typically colonizes a broad spectrum of fast-flowing lotic and lentic waterbodies (Raab, 2006). Although *P. pennipes* was distributed over the entire study area, particularly high abundances could be observed at Kleine Binn and Hagen. This observation is in line with abundance data acquired through a dragonfly survey of Orth an der Donau conducted by Raab (2000). Kl. Binn is a fairly broad side arm characterized by steep side banks featuring large trees. *P. pennipes* is one of few species who uses overhanging tree branches on river banks for perching. Floating dead wood or macrophytes are used for oviposition (Raab, 2006). These characteristics make Kl. Binn/Hagen a very suitable habitat for *P. pennipes*.

In comparison to most other zygopterans recorded in the study area, *Platycnemis pennipes* dispersed over long distances. Individuals were observed on meadows of up to 750 meters away from waterbodies. Although, *Platycnemis pennipes* was still more abundant on meadows which were in closer vicinity to waterbodies, this finding is quite remarkable. High abundance of *P. pennipes* on meadows, in comparison to other zygopterans, could be the response to intraspecific competition, due to high densities of *P. pennipes* at waterbodies, forcing subdominant individuals to disperse. Another reason for long-distance movements observed in *P. pennipes,* as compared to other zygopterans, is that this species is very opportunistic in terms of habitat selection. Since *P. pennipes* reproduces at slow-flowing lotic waterbodies but also lentic waterbodies, movements over longer distances do not put them at risk in terms of finding a suitable habitat as it would for other species that are bound to specific waterbodies (Raab, 2006).

Apart from *Platycnemis pennipes*, *Sympecma fusca* was the only Zygoptera species in the study area that was recorded at distances from waterbodies over 600 meters. All other zygopterans moved less than 400 meters (*Ischnura elegans, Lestes viridis* and *Lestes sponsa*). A study investigating dispersal of *I. elegans* between suitable waterbodies reported that the majority of the individuals studied did not leave the waterside and dispersed less than 5 m during adult life. Our study observed dispersal by *I. elegans* of up to 345 meters, however, only four individuals were found on meadows, suggesting that the majority of individuals do not disperse long distances. However, it has to be noted that different biotic and abiotic parameters apply in dispersal between waterbodies and dispersal to terrestrial habitats. Therefore, comparisons made between existing studies investigating dispersal between waterbodies and this study have to be treated with caution.

Our results are not consistent with findings made by Angelibert and Giani (2003) who studied dispersal behaviour of *C. puella.* While our results suggest that this species does not move long distances, they recorded that a fairly high percentage of *C. puella* dispersed over distances of more than 700 meters. *C. puella* was not observed on any of the meadows in our study area, whatever distance.

Sympetrum species also dispersed fairly long distances and occurred frequently on meadows. All three species, recorded during this study, moved distances of up to 750 meters and were quite evenly distributed over the study area. However, only *Sympetrum striolatum* was observed on the levee. Some observational findings revealed that *Sympetrum* species used temporal water patches for oviposition at site M16 caused by a flooding event in July. Surely, such water patches that merely sustained for two weeks, are not suitable for larval development and could be regarded as ecological traps (Hykel, et al., 2016).

Management implications

A number of species observed in the study area are classified ‘vulnerable’ according to the Austrian’s Red List of dragonflies (Raab, 2007). Among them were *Sympecma fusca, Coenagrion hastulatum, Gomphus vulgatissimus, Aeshna affinis, Aeshna isoceles,* and *Brachytron pretense.*

Since effective management of threatened dragonflies must take into account ecological requirements of dragonflies at all stages of their life cycle (Corbet, 1999), conservation measures of dragonflies should not only concentrate on aquatic habitats but also consider surrounding terrestrial habitats (Hykel, et al., 2016). Dragonflies spend considerable time away from waterbodies (Corbet, 1999) and, as demonstrated in this study, respond positively to rich vegetation structure on meadows. In order to maintain plant diversity and to avoid encroachment of shrubs, meadows in the DANP are mown twice annually (Nationalpark Donau-Auen, 2009). It is widely assumed that mowing affects dragonfly abundance. Lack of suitable areas for roosting during night-time or shelter during inclement weather can be the result of lower abundances (Rouquette & Thompson, 2007). Recently mown habitats are largely avoided by dragonflies (Dolný, et al., 2014; Sternberg & Sternberg, 2004; Wildermuth, 2012). Mowing can increase mortality considerably, especially if mowing is done when odonates are inactive during cloudy or cold weather or periods of rain or high wind (Dolný & Holuŝa, 2008).

Effective conservation of threatened dragonflies must therefore take into account species' period of emergence; mowing regime on meadows located in close vicinity to habitats where the focal dragonfly species is present must be adapted so that first mowing is done before the emergence of adults. The second mowing should be done after the majority of Odonata completed oviposition (Hykel, et al., 2016). Since the flying season of dragonflies observed in the study area varies significantly between species, fulfilling such requirements seems hardly possible and is possibly highly unpractical. Alternatively, a probably more economical management measure is to maintain mosaic-like mowing regimes (Hykel, et al., 2016).

References

Angelibert, S. & Giani, N., 2003. Dispersal characteristics of three odonate species in a patchy habitat. *Ecography 26*, pp. 13-20.

Bellmann, H., 2013. *Der Kosmos Libellenführer.* Stuttgart: Franchkh-Kosmos Verlag.

Buchwald, R., 1989. Die Bedeutung der Vegetation für die Habitatbindung einiger Libellenarten der Quellmoore und Fließgewässer. *Phytocoenologia 17*, pp. 307-448.

Buchwald, R., 1992. Vegetation and dragonfly fauna - characteristics and examples of biocenological fieldstudies. *Vegetatio 101*, pp. 99-107.

Chovanec, A., 1999. Methoden für die Erhebung und Bewertung der Libellenfauna (Insecta: Odonata) - Eine Arbeitsanleitung. *Anax (2) 1*, pp. 1-22.

Chovanec, A. & Waringer, J., 2001. Ecological integrity of river-floodplain systems – assessment by dragonfly surveys (Insecta: Odonata). *Regulated Rivers: Research & Management, 17*, p. 493–507.

Chovanec, A., Waringer, J., Raab, R. & Laister, G., 2004. Lateral connectivity of a fragmented large river system: assessment on a macroscale by dragonfly surveys (Insecta: Odonata). *Aquatic Conservation: Marine and Freshwater Ecosystems, 14*, p. 163–17.

Chwala, E. & Waringer, J., 1996. Association patterns and habitat selection of dragonflies (Insecta: Odonata) at different types of Danubian backwaters at Vienna, Austria. *Arch. Hydrobiol. Suppl 115*, pp. 45-60.

Clarke, K. R. & Gorley, R. N., 2015. *PRIMER v7: User Manual/Tutorial.* Plymouth, 296pp: PRIMER-E.

Clark, T. E. & Samways, M., 1996. Dragonflies (Odonata) as indicators of biotope quality in the Kruger National Park, South Africa. *Journal of Applied Ecology, 33*, p. 1001–1012.

Colwell, R., 2013. *EstimatesS 9.1.0 User's Guide.* [Online] Available at: http://viceroy.colorado.edu/estimates/ [Accessed 26 03 2017].

Colwell, R. K., 2013. *EstimateS 9.1.0.* University of Connecticut, Storrs, CT 06869-3043, USA.

Conrad, K. F. et al., 1999. Dispersal Characteristics of Seven Odonate Species in an Agricultural Landscape. *Ecography 22 (5)*, pp. 524-531.

Corbet, P., 1999. *Dragonflies: Behaviour and Ecology of Odonata.* Colchester: Harley Books.

Corbet, P. S., 1980. Biology of Odonata. *Annual Review of Entomology 25*, pp. 189-217.

Cordoba-Aguilar, A., 1993. Population structure in Ischnura denticollis (Burmeister) (Zygoptera: Coengrionidae). *Odonatologica 22*, pp. 455-464.

Dijkstra, K., 2014. *Libellen Europas: Der Bestimmungsführer..* Bern: Haupt Verlag.

Dolný, A. et al., 2014. Home range, movement, and distribution patterns of the threatened dragonfly Sympetrum depressiusculum (Odonata: Libellulidae): A thousand times greater territory to protect?. *PLos ONE 9*, pp. 1-10.

Dolný, A. & Holuŝa, O., 2008. Sympetrum depressiusculum. In: A. Dolný, et al. eds. *Vážky České republiky: ekologie, ochrana a rozšíření. [The Dragonflies of the Czech Republic: Ecology, Conservation and Distribution].* Vlašim: ČSOP, pp. 556-561.

Foote, A. L., 2005. Odonates as biological indicators of grazing effects on Canadian prairie wetlands.. *Ecol. Entomol. 30*, pp. 273-283.

Garrison, R. W., 1978. A mark-recapture study of imaginal Enallagma cyathigerum (Charpentier) and Argia vivida Hagen (Zygoptera: Coenagrionidae). *Odonatologica 7*, pp. 223-236.

Hykel, M., Harabis, F. & Dolny, A., 2016. Assessment of the quality of the terrestrial habitat of the threatened dragonfl y, Sympetrum depressiusculum (Odonata: Libellulidae). *European Journal of Entomology (113)*, pp. 476-481.

Kennedy, C., 1917. Notes on the life history and ecology of the dragonflies (Odonata) of central California and Nevada. *Proc. U.S. Natl. Mus. 52*, pp. 483-635.

Kirkton, S. D. & Schultz, T. D., 2001. Age-specific behavior and habitat selection of adult male damselflies, Caloperterix maculata (Odonata: Calopterygidae). *J. Insect Behavior 14*, pp. 545-556.

Lenz, N., 1991. The importance of abiotic and biotic factors for the structure of odonate communities of ponds (Insecta: Odonata). *Faun. Ökol. Mitt. 6*, pp. 175-189.

Marden, J. H. & Rowan, B., 2000. Growth, differential survival, and shifting sex ratio of free-living Libellula pulchella (Odonata: Libelluidae) dragonflies during adult maturation. *Annals of the Entomological Society of America 93*, pp. 452-458.

McCauley, J. S., 2010. Body size and social dominance influence breeding dispersal in male Pachydiplax longipennis (Odonata). *Ecological Entomology 35*, pp. 377-385.

McCauley, S. J., 2006. The effects of dispersal and recruitment limitation on community structure of odonates in artificial ponds. *Ecography 29*, pp. 585-595.

McPeek, M. A., 2008. Ecological factors limiting the distributions and abundances of Odonata. In: A. Córdoba-Aguilar, ed. *Dragonfies & Damselflies: Model Organisms for Ecological and Evolutionary Research.* Oxford: Oxford University Press, pp. 51-62.

Moore, N., 1991. Male Sympetrum striolatum (Charp.) "defends" a basking spot rather than a particular locality (Anisoptera: Libellulidae). *NtO 3*, p. 112.

Moore, N. W., 1954. On the dispersal of the Odonata. *Proc. Bristol Nat. Soc. 28*, pp. 407-417.

Moore, N. W., 1964. Intra- and interspecific competition among dragonflies (Odonata). *J. Animal Ecology 33*, pp. 49-71.

Nationalpark Donau-Auen, 2009. *Managementplan Nationalpark Donau-Auen 2009-2018.* Orth an der Donau: Available at:

http://www.donauauen.at/dateien/2216_Managementplan_download_1.12.09.pdf [Accessed 06 03 2017]

Nationalpark Donau-Auen, 2011-2017. *Nationalpark - Donau Auen.* [Online] Available at: http://www.donauauen.at/?area=nationalpark&subarea=numbers [Accessed 06 03 2017].

Parr, M. J., 1973. Ecological studies of Ischnura elegans (Vander Linden) (Zygoptera: Coenagrionidae). II. Survivorship, local movements and dispersal. *Odonatologica 2 (3)*, pp. 159-174.

Perry, T., Perry, M. & Perry, J., 1977. Swarming of dragonflies noted at Drag Lake, Ontario. Can.. *Field-Nat. 91*, pp. 97-98.

Raab, R., 2000. Die Libellenfauna in den Maßnahmenbereichen Untere Lobau und Orth. *Berichte des Nationalpark Donauauen*, p. 74 pp..

Raab, R., 2006. Rote Liste der Libellen Österreichs. In: R. Raab, A. Chovanec & J. Pennerstorfer, eds. *Libellen Österreichs.* Wien, New York: Springer, pp. 325-334.

Raab, R., 2006. Verbreitung und Ökologie der Libellenarten in Österreich. In: R. Rainer, A. Chovanec & J. Pennersdorfer, eds. *Atlas der Libellen Österreichs.* Umweltbundesamt Wien: SpringerWienNewYork, pp. 59-256.

Raab, R., 2007. Rote Liste der gefährdeten Libellen Österreichs. In: Umweltbundesamt, ed. *Libellen Österreichs.* Wien, NewYork: Springer, p. 343.

Raab, R. & Chwala, E., 1997. *Rote Liste ausgewählter Tiergruppen Niederösterreichs - Libellen (Insecta: Odonata),* Wien: Amt der NÖ Landesregierung, Abteilung Naturschutz.

Reckendorfer, Walter. 2002. Shape-Files: Gewässersystem Nationalpark Donau-Auen: Donau und Seitenarme im Bereich östlich der Donau. Format: shp, Quelle: Luftbildinterpretation 1999, Bereich: NPDA, Referenzsystem: GK 34 EPSG-Code.

Rouquette, R. J. & Thompson, D., 2007. Roosting site selection in the endangered damselfly, Coenagrion mercuriale, and implications for habitat design. *J. Insect Conservation 11*, pp. 187-193.

Schindler, M., Fesl, C. & Chovanec, A., 2003. Dragonfly associations (Insecta: Odonata) in relation to habitat variables: a multivariate approac. *Hydrobiologia, 497*, pp. 169–180.

Schmidt, E., 1985. Habitat inventarization, characterization and bioindication by a "representative spectrum of Odonata species (RSO). *Odonatologica, 14*, pp. 127-133.

Schneeweihs, S., 2016. Effects of lateral hydrological connectivity in floodplain systems of dragonfly (Odonata) communities in the Danube Floodplains National Park, Austria. *Nationalpark Donau-Auen - Wissenschaftliche Reihe (50)*, pp. 1-37.

Schulz, H., 2006. *Die Libellenfauna am Fadenbach zwischen Orth und Eckartsau,* Wien: Österreichische Bundesforste AG.

Staufer, M. & Schulze, C. H., 2011. Diversität und Struktur von Libellengemeinschaften an Augewässern in den March-Auen. *Wissenschaftliche Mitteilungen des Niederösterreichischen Landesmuseum 22*, pp. 171-202.

Sternberg, K. & Buchwald, R., 2000. *Die Libellen Baden Württembergs. Band 2: Großlibellen (Anisoptera).* Stuttgart: Eugen Ulmer.

Sternberg, K. & Sternberg, M., 2004. Change of species composition and increase migration of two running waters. *Libellula 23*, pp. 1-43.

Stetter, C., 1996. Colonisation and dispersal patterns of banded (Calopterix splendens) and beautiful demoiselles (C. virgo) (Odonata: Calopterygidae) in south-east German streams. *Eur. J. Entomol. 93*, pp. 579-593.

Suhonen, J., Rantala, M. J. & Honkavaara, J., 2008. Territoriality in odonates. In: A. Córdoba-Aguilar, ed. *Dragonflies & Damselflies: Model Organisms for Ecological and Evolutionary Research.* Oxford: Oxford University Press, pp. 203-217.

Taylor, L. R., 1986. The four kinds of migration. In: W. Danthanarayana, ed. *Insect flight: dispersal and migration.* Berlin: Springer-Verlag, pp. 265-280.

Thompson, D. J., 1991. Sizeb-based dispersal prior to breeding in a damselfly: conflicting evidence from a natural population. *Oecologia 87*, pp. 600-601.

Tockner, K. et al., 1999. Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river-floodplain system (Danube, Austria). *Freshwater Biology, 41*, pp. 521-535.

Tynkkynen, K., Kotiaho, J. S. & Svensson, E. I., 2008. Interspecific interactions and premating reproductive isolation. In: A. Córdoba-Aguilar, ed. *Dragonflies & Damselflies: Model Organisms for Ecological and Evolutionary Research.* Oxford: Oxford University Press, pp. 139-152.

Utzeri, C., Carchini, G., Falchetti, E. & Belfiore, C., 1988. Aspects of demography in Lestes barbarus (Fabr.) and Lestes virens vestalis Ramb. (Zygoptera: Lestidae). *Odonatologica 17*, pp. 107-114.

QGIS Development Team, 2017. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org. QGIS Development Team, 2017. QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org.

Wildermuth, H., 1994. Habitatselektion bei Libellen.. *Adv. Odonatol. 6*, pp. 223-257.

Wildermuth, H., 2012. Extensively used meadows as habitat for maturation, forage and copulation of Coenagrion puella and Enallagma cyathigerum (Odonata: Coenagrionidae). *Libellula 31*, pp. 223-235.

Appendix

Table A1. Abbreviation of study sites, geographic coordinates, names of meadows, location: S – south of Marchfeld levee, N – north of Marchfeld levee, L – situated on Marchfeld levee, area of study site in ha.

Site	GPS Coordinates		Meadow name	Location	Area (ha)
M1	48.131053	16.668250	Dänekegrund	S	2.17
M2	48.130833	16.673639	Forstmeisterwiese 2	S	1.53
M3	48.134556	16.670861	Marchfeldschutzdam. Schaftrieb	L	5.05
M4	48.138861	16.670389	Jankwiese	N	2.11
M5	48.138889	16.679528	Obere Heustadlwiese. Heustadlwiese	N	8.87
M6	48.138667	16.686778	Heustadlwiese	N	2.38
M7	48.143556	16.685739	Voglwiese	N	1.09
M8	48.142139	16.690417	Zweiter Grund. Heustadlweg. Wildacker	N	2.10
M9	48.137889	16.695583	Zweiter Grund 1	N	0.73
M10	48.133306	16.697528	Tierwiese 2	S	8.33
M11	48.129944	16.700089	Tierwiese 1	S	0.87
M12	48.134167	16.683586	Marchfeldschutzdam ab 23-24 km	L	3.26
M13	48.133989	16.695000	Marchfeldschutzdam ab 24 m	L	4.45
M14	48.133558	16.705500	Alter Sportplatz 1	S	2.22
M15	48.130278	16.678083	Neubruch	S	7.48
M16	48.128194	16.698444	Gernsteinerin 2	S	0.75
W1	48.124833	16.689917	Große Binn	S	
W2	48.129639	16.698778	Kleine Binn	S	
W3	48.131222	16.682500	Kleine Binn	S	
W4	48.131389	16.667542	Hagen	S	
W5	48.138111	16.682889	Baggerteich	N	
W6	48.141972	16.684761		N	
W7	48.136806	16.704750	Fadenbach	N	
W8	48.130083	16.705667	Fadenbach	S	

Table A2. Closest distance of meadows to waterbody sites and structural variables of meadow sites; location: S – south of Marchfeld levee, N – north of Marchfeld levee, L – situated on Marchfeld levee.

Site	Meadow name	Location	Distance to closest waterbody (m)	Closest waterbody	Structural diversity of forest margin	SDI index
M1	Dänekegrund	S	109	Kl. Binn	1	1.10
M2	Forstmeisterwiese 2	S	317	Kl. Binn	1	1.09
M3	Marchfeldschutzdam. Schaftrieb	L	560	Kl. Binn	1	1.00
M4	Jankwiese	N	1205	Kl. Binn	3	1.09
M5	Obere Heustadlwiese. Heustadlwiese	N	403	Baggerteich	2	1.11
M6	Heustadlwiese	N	424	Baggerteich	2	1.02
M7	Voglwiese	N	330	Fadenbach	2	1.04
M8	Zweiter Grund. Heustadlweg. Wildacker	N	645	Fadenbach	1	1.10
M9	Zweiter Grund 1	N	750	Fadenbach	2	1.02
M10	Tierwiese 2	S	440	Kl. Binn	2	1.03
M11	Tierwiese 1	S	170	Kl. Binn	2	1.16
M12	Marchfeldschutzdam ab 23-24 km	L	532	Kl. Binn	1	1.00
M13	Marchfeldschutzdam ab 24 m	L	504	Kl. Binn	1	1.00
M14	Alter Sportplatz 1	S	95	Fadenbach	2	1.01
M15	Neubruch	S	134	Kl. Binn	3	1.07
M16	Gernsteinerin 2	S	268	Kl. Binn	3	1.15

Table A3. Species-specific distances according to distance to closest waterbody.

Suborder Zygoptera	**Max. distance moved (m)**
Family Calopterygidae	
Calopteryx splendens (Harris, 1782)	only observed at waterbody
Family Lestidae	
Lestes viridis (Vander Linden, 1825)	268
Lestes sponsa (Hansemann, 1823)	109
Sympecma fusca (Vander Linden, 1820)	645
Family Coenagrionidae	
Coenagrion hastulatum (Charpentier, 1825)	only observed at waterbody
Coenagrion puella (Linnaeus, 1758)	only observed at waterbody
Erythromma najas (Hansemann, 1823)	only observed at waterbody
Erythromma viridulum (Charpentier, 1840)	only observed at waterbody
Ischnura elegans (Vander Linden, 1820)	317
Ischnura pumilio (Charpentier, 1825)	only observed at waterbody
Family Platycnemididae	
Platycnemis pennipes (Burmeister, 1839)	750
Suborder Anisoptera	
Family Gomphidae	
Gomphus vulgatissimus (Linnaeus, 1758)	only observed at waterbody
Family Aeshnidae	
Aeshna affinis (Vander Linden, 1820)	1205
Aeshna cyanea (Müller, 1764)	317
Aeshna grandis (Linnaeus, 1758)	645
Aeshna isoceles (Müller, 1767)	1205
Aeshna mixta (Latreille, 1805)	1205
Anax imperator (Leach, 1815)	1205
Anax parthenope (Selys, 1883)	424
Brachytron pratense (Müller, 1764)	170
Family Corduliidae	
Somatochlora metallica (Vander Linden, 1825)	only observed at waterbody
Family Libellulidae	
Crocothemis erythraea (Brullé, 1832)	317
Libellula depressa (Linnaeus, 1758)	1205
Libellula quadrimaculata (Linnaeus, 1758)	only observed at waterbody
Orthetrum albistylum (Selys, 1841)	440
Orthetrum cancellatum (Linnaeus, 1758)	1205
Sympetrum sanguineum (Müller, 1764)	750
Sympetrum striolatum (Charpentier, 1840)	750
Sympetrum vulgatum (Linnaeus, 1758)	750

Table A4. Conservation status according to Red List *(Raab & Chwala, 1997)* and *(Raab, 2007)*. Categories of Red List Austria: EN – endangered, VU – vulnerable, NT – near threatened, LC – least concern; Rest List Lower Austria: 1 – vom Austerben bedroht (critically endangered), 2 – stark gefährdet (strongly endangered), 3 – gefährdet (endangered), 4 – potenziell gefährdet (potentially endangered), 5 – Gefährdung anzunehmen (vulnerability assumed), 6 – Forschungsbedarf (further research is necessary to determine vulnerability status), + not endangered.

Suborder Zygoptera	**Conservation status**	
Family Calopterygidae	RL A (Raab 2007)	RL LA (Raab 1997)
Calopteryx splendens (Harris, 1782)	NT	4
Family Lestidae		
Lestes viridis (Vander Linden, 1825)	LC	+
Lestes sponsa (Hansemann, 1823)	LC	+
Sympecma fusca (Vander Linden, 1820)	VU	3
Family Coenagrionidae		
Coenagrion hastulatum (Charpentier, 1825)	VU	1
Coenagrion puella (Linnaeus, 1758)	LC	+
Erythromma najas (Hansemann, 1823)	NT	4
Erythromma viridulum (Charpentier, 1840)	LC	4
Ischnura elegans (Vander Linden, 1820)	LC	+
Ischnura pumilio (Charpentier, 1825)	NT	2
Family Platycnemididae	LC	+
Platycnemis pennipes (Burmeister, 1839)		
Suborder Anisoptera		
Family Gomphidae		
Gomphus vulgatissimus (Linnaeus, 1758)	VU	3
Family Aeshnidae		
Aeshna affinis (Vander Linden, 1820)	VU	3
Aeshna cyanea (Müller, 1764)	LC	+
Aeshna grandis (Linnaeus, 1758)	LC	+
Aeshna isoceles (Müller, 1767)	VU	1
Aeshna mixta (Latreille, 1805)	LC	+
Anax imperator (Leach, 1815)	LC	+
Anax parthenope (Selys, 1883)	LC	2
Brachytron pratense (Müller, 1764)	VU	2
Family Corduliidae		
Somatochlora metallica (Vander Linden, 1825)	LC	+
Family Libellulidae		
Crocothemis erythraea (Brullé, 1832)	LC	6
Libellula depressa (Linnaeus, 1758)	LC	+
Libellula quadrimaculata (Linnaeus, 1758)	LC	3
Orthetrum albistylum (Selys, 1841)	LC	6
Orthetrum cancellatum (Linnaeus, 1758)	LC	+
Sympetrum sanguineum (Müller, 1764)	LC	+
Sympetrum striolatum (Charpentier, 1840)	LC	+
Sympetrum vulgatum (Linnaeus, 1758)	LC	+

Table A5. Species that allowed sex determination in the field

Suborder Anisoptera
Aeshna affinis (Vander Linden, 1820)
Aeshna cyanea (Müller, 1764)
Anax imperator (Leach, 1815)
Anax parthenope (Selys, 1883)
Brachytron pratense (Müller, 1764)
Libellula depressa (Linnaeus, 1758)
Libellula quadrimaculata (Linnaeus, 1758)
Orthetrum cancellatum (Linnaeus, 1758)
Sympetrum sanguineum (Müller, 1764)
Sympetrum striolatum (Charpentier, 1840)
Sympetrum vulgatum (Linnaeus, 1758)

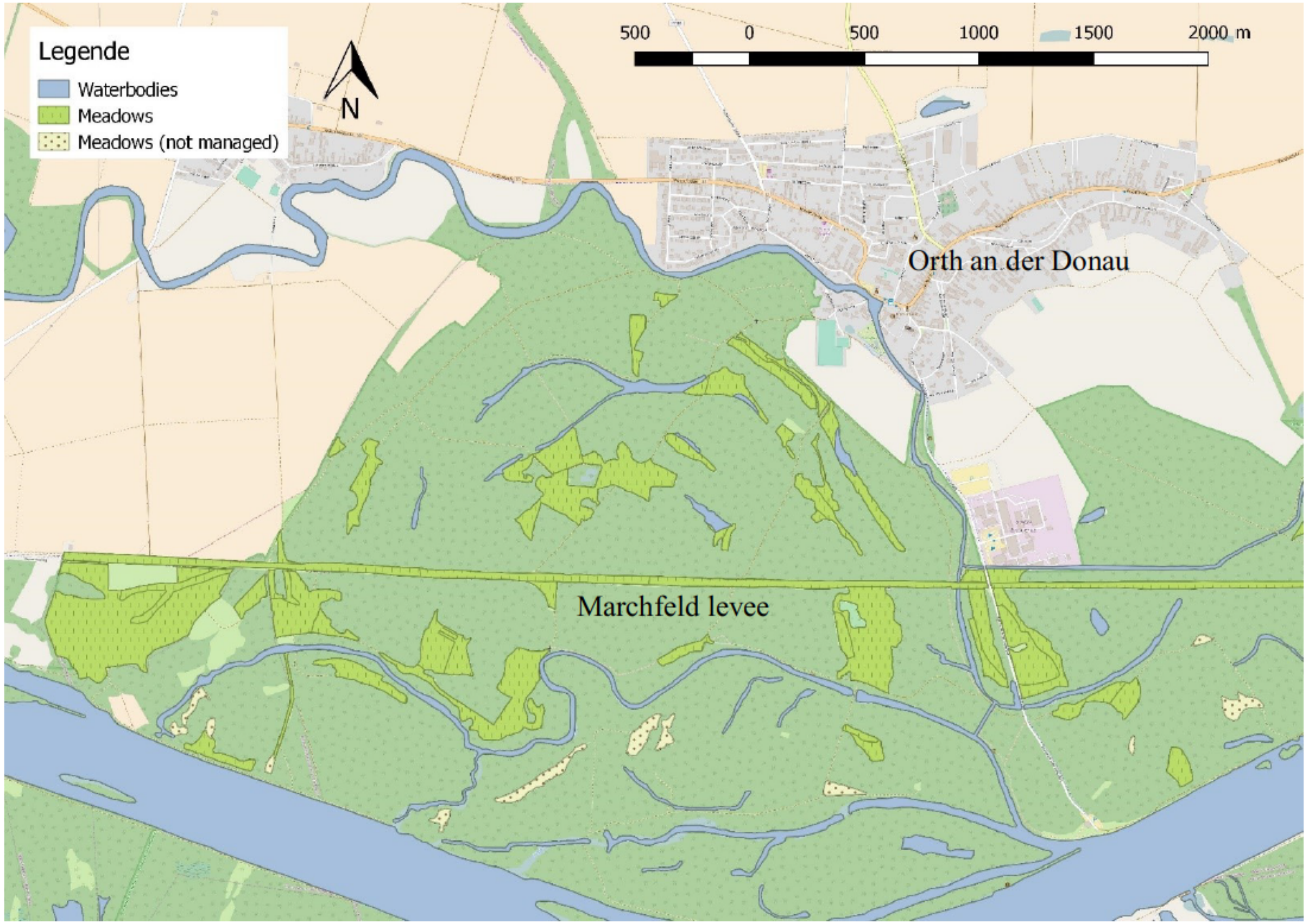

Figure A6. Map of the study area. Different coloration indicates waterbodies (blue), forest (green) and meadows (light green).

Table A7. Abundance of species at individual transects. Colors represent abundance data: grey boxes indicate zero observations, yellow boxes indicate abundance between 1-10 individuals, orange boxes indicate abundances between 11-20, red boxes 21-50, green boxes 51-70, purple boxes 71-100, blue boxes 101-130.

Species																								
Suborder Zygoptera	**M1**	**M2**	**M3**	**M4**	**M5**	**M6**	**M7**	**M8**	**M9**	**M10**	**M11**	**M12**	**M13**	**M14**	**M15**	**M16**	**W1**	**W2**	**W3**	**W4**	**W5**	**W6**	**W7**	**W8**
Family Calopterygidae																								
Calopteryx splendens (Harris, 1782)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	7	1	0	0	0	0
Family Lestidae																								
Lestes viridis (Vander Linden, 1825)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0
Lestes sponsa (Hansemann, 1823)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sympecma fusca (Vander Linden, 1820)	0	0	0	0	2	0	2	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Family Coenagrionidae																								
Coenagrion hastulatum (Charpentier, 1825)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
Coenagrion puella (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	19	10	16	64	8
Erythromma najas (Hansemann, 1823)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	5	4	0	16
Erythromma viridulum (Charpentier, 1840)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	7	0	0	10
Ischnura elegans (Vander Linden, 1820)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0	4	2	6	6	32	19	0	0
Ischnura pumilio (Charpentier, 1825)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0
Family Platycnemididae																								
Platycnemis pennipes (Burmeister, 1839)	6	16	13	0	2	9	1	5	10	23	41	12	11	13	23	46	20	117	57	39	59	10	4	0

Legend	
⬜	0
🟨	1-10
🟧	11-20
🟥	21-50
🟩	51-70
🟪	71-100
🟦	101-130

Suborder Anisoptera	**M1**	**M2**	**M3**	**M4**	**M5**	**M6**	**M7**	**M8**	**M9**	**M10**	**M11**	**M12**	**M13**	**M14**	**M15**	**M16**	**W1**	**W2**	**W3**	**W4**	**W5**	**W6**	**W7**	**W8**
Family Gomphidae																								
Gomphus vulgatissimus (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	1	0	0	0
Family Aeshnidae																								
Aeshna affinis (Vander Linden, 1820)	0	0	0	5	2	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	1	1
Aeshna cyanea (Müller, 1764)	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	0
Aeshna grandis (Linnaeus, 1758)	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aeshna isoceles (Müller, 1767)	1	1	12	41	13	1	6	3	7	1	0	15	25	0	0	1	0	0	0	2	0	1	0	2
Aeshna mixta (Latreille, 1805)	0	1	11	4	1	0	1	1	1	0	3	13	28	2	1	0	0	0	0	1	1	0	0	4
Anax imperator (Leach, 1815)	1	4	5	2	4	2	2	4	2	1	1	3	0	3	2	2	1	0	0	4	4	1	0	2
Anax parthenope (Selys, 1883)	0	0	0	0	0	1	0	0	0	0	2	0	0	0	1	0	1	0	0	0	0	0	0	0
Brachytron pratense (Müller, 1764)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
Family Corduliidae																								
Somatochlora metallica (Vander Linden, 1825)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	2
Family Libellulidae																								
Crocothemis erythraea (Brullé, 1832)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	0	0	0
Libellula depressa (Linnaeus, 1758)	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Libellula quadrimaculata (Linnaeus, 1758)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Orthetrum albistylum (Selys, 1841)	0	0	0	0	3	0	1	0	0	1	0	0	0	1	0	4	0	0	0	0	0	0	0	0
Orthetrum cancellatum (Linnaeus, 1758)	3	2	6	2	0	0	0	4	7	0	1	2	6	1	3	3	5	0	0	8	25	9	0	0
Sympetrum sanguineum (Müller, 1764)	8	0	0	0	0	0	1	2	6	0	2	0	0	4	1	12	1	0	0	14	3	2	1	5
Sympetrum striolatum (Charpentier, 1840)	3	1	1	0	1	2	1	4	2	2	0	1	3	1	2	4	0	1	0	0	6	4	2	0
Sympetrum vulgatum (Linnaeus, 1758)	7	4	0	0	3	0	0	2	2	3	2	1	0	0	9	6	2	2	2	4	5	6	12	4
Total	**30**	**31**	**48**	**55**	**29**	**15**	**15**	**31**	**37**	**31**	**53**	**47**	**76**	**25**	**42**	**80**	**37**	**135**	**72**	**133**	**169**	**76**	**84**	**54**