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Stefan Schneeweihs

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Effects of lateral hydrological connectivity in floodplain systems on dragonfly (Odonata) communities in the Danube Floodplains National Park, Austria

Stefan Schneeweihs
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Abstract

Adult dragonflies were sampled at 31 sites along floodplain channels and the Danube River in the Danube Floodplains National Park in Eastern Austria between May and September 2006. A total of 7370 individuals belonging to 33 species were observed. Species richness estimated for individual sites varied between 7 and 25 species. Lateral connectivity of side arms representing the upstream water surface connection between the main Danube river channel and side arms was calculated from the hydrograph. Species richness and community composition differed between sites as response to lateral hydrological connectivity. Effects of side arm connectivity were overriding all other variables: habitat diversity, restoration measures in side arms and spatial proximity of sites. High lateral connectivity decreased total dragonfly species richness, but clearly favoured the presence of rheophilic species.

Hydrological dynamics in the NP have been disturbed by river regulations since the late 19th century causing a trend towards habitat senescence (terrestrialization processes) and a decline in rheophilic species. Recently, the goal of restoration programs is the reconnection of cut-off side arms and enhancement of lateral connectivity in order to favour rheophilic species. Predictive tools and assessments of the effects of enhanced lateral connectivity are therefore needed. This study quantifies the response of odonate communities to lateral connectivity and provides important information for future assessments of effects of restoration projects on European dragonflies.

Zusammenfassung

Von Mai bis September 2006 wurden 31 Standorte entlang von Nebenarmen und des Hauptstroms der Donau im Nationalpark Donau-Auen im Osten Österreichs auf das Vorkommen adulter Libellen untersucht. Insgesamt wurden 7370 Individuen aus 33 Arten beobachtet. Der für einzelne Standorte geschätzte Artenreichtum lag zwischen 7 und 25 Arten. Aus den Pegeldaten der Donau wurde die Anbindungsintensitäten der Nebenarme als Dauer der Oberflächen-Wasserverbindung zwischen Hauptstrom und Nebenarm an der flussaufwärts gelegenen Einströmöffnung errechnet. Artenreichtum und Artenzusammensetzung unterschieden sich zwischen Standorten verschiedener hydrologischer Anbindungsintensität. Die Anbindungsintensität der Nebenarme erklärte den beobachteten Artenreichtum und Ähnlichkeiten in der Artenzusammensetzung besser als strukturelle Habitatvielfalt und Restaurationsmaßnahmen in den Nebenarmen. Hohe Anbindungsintensität führte zu einer Abnahme des Libellenartenreichtums, begünstigte aber die Besiedlung durch strömungsliebende Arten.

Die hydrologische Dynamik der Donau im Bereich des heutigen Nationalparks wurde im späten 19. Jahrhundert durch Regulierungmaßnahmen stark beeinträchtigt, was zu Verlandungsprozessen sowie einem Rückgang strömungsliebender Arten führte. Durch Renaturierungsmaßnahmen – wie die Anbindung abgeschnittener Nebenarme – wird aktuell versucht, die ehemals hohe hydrologische Dynamik wiederherzustellen und damit günstigere Bedingungen für strömungsliebende Arten zu schaffen. Um die Auswirkungen solcher Restaurationsmaßnahmen besser abschätzen zu können, untersucht diese Arbeit den Einfluss der Anbindungsintensität von Augewässern auf Libellengemeinschaften. Die Ergebnisse erlauben eine bessere Beurteilung des Erfolgs solcher Renaturierungsmaßnahmen aus libellenkundlicher Sicht.

Key words: Species richness, species composition, river restoration, connectivity, rheophilic species, conservation

Introduction

The role of dragonflies as reliable indicators for habitat quality and characteristics has been stressed in numerous recent studies (Clark & Samways 1996, Kinvig & Samways 2000, Chovanec & Waringer 2001, Sahlén & Ekestubbe 2001, Chovanec et al. 2004, D'Amico et al. 2004, Bried et al. 2007). Their semi-aquatic life style allows the assessment of the conservation status of both aquatic and adjacent terrestrial habitats (Schindler et al. 2003). Dragonfly larvae inhabit a wide array of freshwater systems, but the environmental demands of single species can be specific. Particularly these stenotopic species become affected by anthropogenic habitat alterations causing habitat loss, fragmentation and isolation (Corbet 1999, Rouquette & Thomson 2007, Clausnitzer 2003, Dudgeon et al. 2006). In dragonfly communities of streams in Finland, for instance, the local extinction risk proved to be highest for habitat specialists and high for true lotic species (Korkeamäki & Suhonen 2002).

River-floodplain systems can include habitats ranging from lentic (oxbow lakes) and semi-lentic to lotic water bodies (side arms) with variable hydrological dynamics (Amoros & Bornette 2002, Ward et al. 1999, Lasne et al. 2007) on a relatively small spatial scale and thus provide potential habitats for various dragonfly species with different habitat demands (Tockner et al. 1999b, Chovanec et al. 2004). The Danube Floodplains National Park (DFNP) represents one of the last quasi free flowing stretches of the Danube in Austria. However, bank regulation and disconnection of side channels has changed flow dynamics and other physical parameters. Freshwater biodiversity is globally threatened by human activities (Dudgeon et al. 2006) and flow modification and disconnection of side arms due to regulation have considerably influenced biodiversity in the Danube floodplains (Ward et al. 1999). Rejuvenation via hydrological dynamics is a key attribute of floodplain ecosystems. Disconnection causes senescence (terrestrialization processes) and suitable habitats for species related to dynamic conditions become scarce (Ward et al. 1999, Brunke 2002).

During the last decade the "Danube Restoration Project" has partially restored former dynamics and enhanced lateral hydrological connectivity of selected floodplain channels (Tockner et al. 1999b). With the implementation of the "Integrated River Engineering Project" (IREP) of the Austrian Federal Waterway Agency further reconnections are expected in order to create favourable conditions for rheophilic species (Reckendorfer et al. 2006). Such changes in hydrological connectivity may cause shifts in dragonfly community structure. Knowledge on dragonfly community structure in floodplain systems and their relation to environmental factors may be helpful for predictions of community response, especially of rheophilic species, if such restoration efforts are implemented.

Although the dragonfly fauna of the DFNP is well known and has been the subject of previous studies that took into account water dynamics and different habitat types shaped by hydrological connectivity (Chovanec & Waringer 2001, Chovanec et al. 2004), quantitative data about the relationship between hydrological connectivity and the distribution of species and composition of species assemblages do not exist. Such information would provide a helpful tool to forecast effects of reconnection of side arms and enhancement of lateral connectivity.

This study investigated dragonfly communities in DFNP floodplain systems and the effect of lateral connectivity on their composition and species distribution with special regard to rheophilic species in order to provide data for future management implications in the study area.

Methods

Study area

The Danube Floodplains National Park (DFNP) is situated in Eastern Austria and forms a narrow stretch of 31 km length along the river Danube from Vienna to the Slovakian border. The highest point of the Danube at the westernmost side of the National Park in Vienna is at 144 m a.s.l., the lowest at 111 m a.s.l. at the border to Slovakia; the average slope of the Austrian section of the Danube is 0.045% (Tockner et al. 1999b). According to the Strahler system the Danube is a ninth-order river and discharge ranges between 800–6000 m^3s^{-1} (annual average approximately 2000 m^3s^{-1}) showing strong seasonal patterns dominated by the influence of alpine tributaries. Average flow velocity is relatively high with 2–2.5 ms^{-1}. There are two discharge peaks, one in late winter as consequence of thaw in the catchment, and one in early summer due to a climax in precipitation (Chovanec et al. 2000, Schultz et al. 2003, Chovanec et al. 2004).

Discharge peaks lead to flood events in the floodplains of the DFNP. However, the river and its adjacent floodplains have been hit by harsh regulation efforts in 1870-1875 that disconnected many side channels and transformed hydrology (Tockner et al. 1999b, Chovanec et al. 2002). The Danube Restoration Project has partially re-established former connectivity via removal of dams and lowering of riverside levees at some side arms in the DFNP (Tockner et al. 1999b) and further reconnections are planned by the Integrated River Engineering Project (Reckendorfer et al. 2006).

Study sites

A total of 31 survey sites were situated in the eastern half of the DFNP between Orth an der Donau (48° 08’ 47’’ N, 16° 42’ 12’’ E) and Hainburg (48° 08’ 52’’ N, 16° 58’ 08’’ E) (Fig. 1) along side arms and the Danube river channel, embedded in floodplain forests with e.g. *Populus*, *Alnus* and *Quercus* that cover large areas of the DFNP. Each site sampled for adult dragonflies represented a 50 m reach of one channel bank. Survey sites were selected according to their lateral hydrological connectivity (see below).

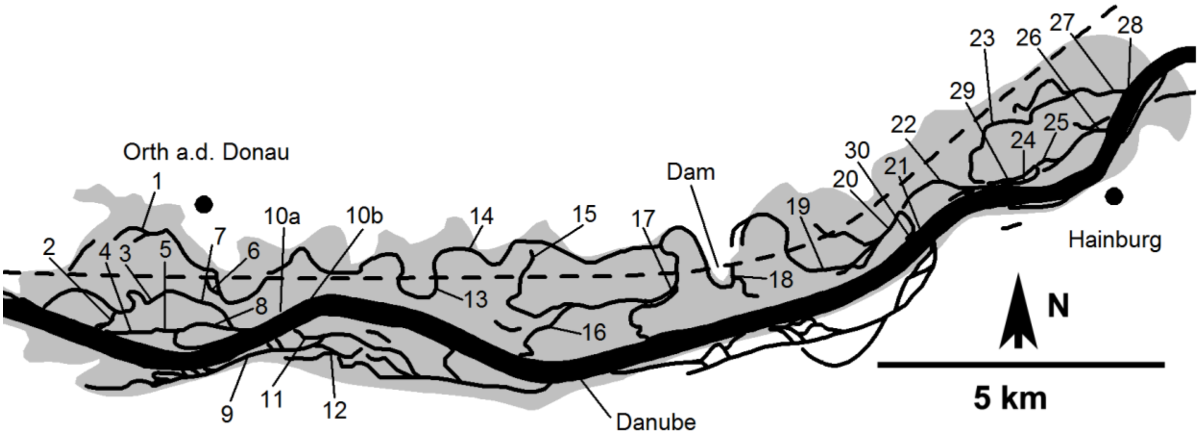

Figure 1: Study area and location of sampling sites. The area of the Danube Floodplains National Park is depicted in grey.

Survey method

Dragonflies were observed with binoculars (8 x 21) or caught with a sweep net (diameter 40 cm). Caught individuals were released after identification. All individuals on the bank and over the water body were recorded, except in channels broader than 10 m, where dragonflies present at the opposite bank were omitted from observation. Exuviae were not systematically searched but recorded when seen by chance.

Surveys at each site lasted from 30 to 60 minutes. Abundance of dragonflies was assessed by estimating the maximum number of individuals observed at the same time. For identification of adults and exuviae identification keys of Dreyer (1986), Bellmann (1993) and Jurzitza (2000) were used.

Each site was visited 7 times. All 31 sites were visited once during one week before the next round of observations started. Order of sites visited on the same day was changed systematically in order to avoid influence of day time on sampling results. Observations were only performed on days with sunny weather conditions and little or no wind speeds. Surveys were conducted between May 16th and September 16th 2006.

Habitat parameters

Biotic habitat variables, especially vegetation, may affect the presence of dragonflies (Corbet 1999, Rantala et al. 2004). Therefore the type and structure of bank vegetation at sites was recorded and assigned to six categories (meadow, reed, woody plants, logs, gravel and sand). Types of water vegetation (floating macrophytes, reed, emergent logs as perch sites) were also recorded. Presence (1) or absence (0) of these types of structures was summarized in an index of habitat diversity (HDI) potentially ranging between 0-9. Actual HDI values for study sites ranged between 1 and 4 (Tab. 1).

Lateral connectivity

Sampling sites were selected according to their lateral connectivity. Lateral hydrological connectivity is defined as the permanent and episodic hydrological upstream-downstream connection of floodplain waterbodies. Lateral hydrological connectivity for instance links the side arms of floodplain systems with the main channel and influences habitat components like flow dynamics, water temperature and substrata composition (Amoros & Bornette 2002). In this study lateral connectivity refers to the upstream surface water connection between the main channel and side arms.

Lateral connectivity was calculated as mean duration of surface water connection between side channels and the main channel in days per year using the hydrograph of Wildungsmauer (www.doris.bmvit.gv.at/pegel_furten/) and height of inflow areas of side channels. Levels of characteristic discharges (mid-water) are known for every stream kilometre and can be compared with the water level relative to mid-water at the hydrograph. Four sites were situated at the Danube main channel, so their duration of lateral connectivity was 365 da^{-1}. Three sites were located offside a flood-protection dam, isolated from flood events and therefore with a lateral connectivity of 0 da^{-1}. Lateral connectivity of the remaining sites ranged between 12 and 228 da^{-1} (Tab. 1).

Lateral connectivity can impact dragonfly development in two ways. Larvae have do deal with the dynamics in discharge and frequency of connectivity. Some species show specific demands in their larval habitats e.g. oxygen level, presence of macrophytes and flow velocity (Osborn & Samways 1996, Kinvig & Samways 2000). For these stenotopic species lateral connectivity will be a determining trait in maintaining self-sustaining populations. On the other hand, adult dragonflies have to preselect their mating and oviposition places on their ability to support development of their offspring, or they may suffer a loss in fitness (Hofmann & Mason 2005, McCauley 2006). Therefore lateral connectivity of two consecutive years was used separately for analysis to incorporate this aspect of site choices already taken by adults in the previous year and the ones that were taken during the actual survey period.

Many species found in this study are univoltine, completing their larval development during one season and reproducing in the following summer (Jurzitza 2000). For these species their larval phase may last from October until September of the following year since oviposition takes place in summer and at the end of September the reproductive season for almost all species has finished or at least passed its peak for late species. So lateral connectivity was computed for the periods October 2004 - September 2005, October 2005 - September 2006, and for the years 2005 and 2006 as well. Connectivity duration in days per year for the respective sites, however, was almost the same and results of tests did not substantially differ between October - September periods and calendar years.

Restoration status

Restoration works have already been implemented at several side arms in the DFNP during the last two decades in order to enhance connectivity of these systems. To test for potential effects of these recent measures on dragonfly communities, species occurrence patterns were compared between unrestored sites (n = 22), and sites restored since 1994 (n = 3) and 2002 (n = 6).

Determination of autochthony of species and species traits

Since adult odonates show high dispersal abilities (Corbet 1999) the status of a species (visitor or autochthonous) at a given site can only be doubtlessly determined by detection of larvae or exuviae. Nonetheless adult dragonflies are the ones that oviposit and their habitat selection acts as a filter on species composition (McCauley 2006, Hofmann & Mason 2005). Therefore, the observation of adults can lead to a rather reliable assessment of their breeding status (Stewart & Samways 1998). In this study, dragonflies showing oviposition behaviour or displaying mating behaviour as well as species that were observed frequently (>1 time) or in great abundances were defined as autochthonous at the respective site (Appendix).

Information about habitat preferences of species (rheophilic or limnophilic) and oviposition (endophytic or exophytic type) were derived from literature (Askew 2004).

Statistical analysis

The completeness of sampled species inventories depends on various variables e.g. identification skills of the observer, stochastic events, and temporal limitation of the survey period. These factors can strongly influence numbers of species recorded at individual survey sites thereby causing potentially a significant underestimation of local species richness. Therefore, additionally to recorded species numbers, species richness was estimated for each site with four different nonparametric estimators (ACE, Chao1, Chao2, Jackknife1). Estimates were calculated with the software package EstimateS 7.0 randomizing the sample order 100 times (Colwell 2006). The median of all estimators was used as measure for species richness of sampling sites because the performances of single estimators were considerably inconsistent between survey sites.

Spearman rank correlations were calculated to test if dragonfly species richness, abundance and proportion of rheophilic species were related to lateral connectivity of side arms. Measures for species richness were number of recorded and autochthonous species and their estimates respectively. Correlations were done for all four connectivity periods and repeated after the exclusion of Danube river sites to test the sole effect of side arm connectivity on species richness.

Relationships between species richness, HDI and restoration status were tested with parametric ANOVAs (type VI) or nonparametric Kruskal-Wallis tests when data were not normally distributed. Post-hoc tests used for pairwise comparisons were Tukey’s HSD test for unequal sample sizes after ANOVAs and a standard multiple range test in nonparametric cases.

Generalized linear models (GLMs) were used to test simultaneously for effects of side arm connectivity and HDI on estimated species richness. The Akaike information criterion was used to identify the order of environmental variables that best explain variation in estimated species richness.

Similarity of species composition was quantified by Bray-Curtis similarities calculated with square root transformed abundances. Non-metric multidimensional scaling (NMDS) plots based on Bray-Curtis similarities were constructed to visualize relationships between sites. Effects of lateral connectivity and habitat diversity (HDI) on species composition (Bray-Curtis similarities) were tested by one-way analyses of similarities (ANOSIM, maximum number of allowed permutations = 999). Therefore, side arms were categorized according to their lateral connectivity into groups of water bodies connected for 0, >0-30, >30-120 and >120 da^{-1} with the Danube river main channel. Danube river sites (connected 365 da^{-1}) represented a category of their own. Sites were also classified according to their HDI (1–4). In a two-way crossed ANOSIM pairwise comparisons of community compositions were made for classes of connectivity and HDI, but isolated (connected 0 da^{-1}; n = 3) and Danube river sites (n = 4) were excluded due to their small number of spatial replicates. A one-way ANOSIM was calculated to test for differences of species composition between sites with a different restoration status (no restoration, 1994, 2002).

A Spearman matrix rank correlation was calculated to test for effects of spatial proximity of sites on species composition. In addition, Euclidian distance matrices between sites were constructed with regard to environmental variables (i.e. lateral connectivity and habitat diversity) in order to establish relationships between faunal and environmental similarity. To correct detected relationships between species composition and habitat variables for spatial autocorrelation, partial Mantel tests were computed with zt software (Bonette & Van de Peer 2002). Bray-Curtis similarities, Spearman matrix rank correlations (with 999 permutations) and ANOSIMs were computed with Primer v5 (Clarke & Gorley 2001). All other statistical analyses were calculated with Statistica 7 (Statsoft 2005).

Results

General results

During this study 7370 individuals belonging to 33 species (11 Zygoptera, 22 Anisoptera) and 8 families (4 Zygoptera, 4 Anisoptera) were observed, representing 66% of the dragonfly fauna known for the DFNP (Raab 2000) and 43% of Austria’s dragonfly fauna (Raab et al. 2006). A total of 30 species were considered to be autochthonous at surveyed sites. Three recorded species, *Coenagrion hastulatum*, *Aeshna isosceles* and *Ophiogomphus cecilia*, were not classified as autochthonous at any of the survey sites.

Table 1: Lateral hydrological connectivity 2006 (da^{-1}), habitat diversity (HDI), and estimated species richness and abundance of dragonflies for all surveyed sites. Completeness of species inventories was calculated as percentage of observed species relative to estimated species richness. Side arms where restoration measures were implemented are indicated by ^{1} (year of implementation: 1994) and ^{2} (2002), respectively.

			All species			Autochthonous species		
Sites	Connectivity	HDI	Individuals	Estimate	Completeness	Individuals	Estimate	Completeness
s1	0	3	291	16	89	288	11	100
s14	0	2	107	14	80	105	10	90
s15	0	2	403	18	88	401	15	93
s13	12	4	399	17	96	399	17	94
s16	12	2	214	10	94	213	8	100
s17	12	3	532	25	73	528	15	93
s18	12	3	400	19	82	397	13	100
s19	12	2	720	21	95	718	18	100
s22	12	4	365	19	81	361	11	100
s23	12	3	251	16	96	250	14	100
s26	12	2	154	7	94	153	6	100
s27	12	3	511	23	79	507	15	93
s30	12	3	371	21	82	369	16	94
s6	12	4	284	22	77	279	12	100
s29	37	2	169	13	87	167	9	100
s24	39	2	56	11	83	54	7	100
s25	39	2	311	19	65	307	8	100
s20	93	3	650	18	83	647	12	100
s12^1	147	3	297	15	82	295	11	91
s9^1	147	1	208	8	88	206	5	100
s11^1	151	2	128	12	78	125	6	100
s4^2	181	1	59	12	77	57	8	88
s5^2	181	3	86	11	86	84	7	100
s8^2	181	1	60	10	70	58	6	83
s2^2	228	3	62	8	95	61	7	100
s3^2	228	2	133	10	99	133	10	100
s7^2	228	2	57	11	63	54	4	100
s10a	365	1	16	8	66	13	2	100
s10b	365	2	18	10	71	17	8	75
s21	365	2	27	7	84	25	4	100
s28	365	2	31	12	69	29	8	75

The most abundant species were *Platycnemis pennipes* and *Sympetrum sanguineum* with 2009 (27% of total counted individuals) and 1017 individuals (14%), respectively. The most frequent species were *Sympetrum sanguineum, S. vulgatum*, *Platycnemis pennipes* and *Ischnura elegans* recorded at 31, 29, 28 and 25 sites, respectively. Rare species recorded at only one site were *Coenagrion hastulatum*, *Epitheca bimaculata*, and *Aeshna isosceles*. Species with records from various survey sites but classified as autochthonous at only one site were *Aeshna cyanea, Crocothemis erythraea* and *Libellula depressa* (Appendix).

Between 5–20 dragonfly species were recorded at individual survey sites. Of these, 2–18 species were classified as locally autochthonous. The completeness of species inventories ranged from 63-99% for recorded species and from 75-100% for autochthonous species (Table 1). Estimated species richness (median of 4 estimators) highly correlated with observed species richness (recorded species: $r_s = 0.94$, $p < 0.0001$; autochthonous species: $r_s = 0.98$, $p < 0.0001$).

Total species richness and richness of autochthonous species

Species richness was significantly related to lateral connectivity for all species (N = 31; recorded richness: $r_s = -0.73$, $p < 0.001$; estimated richness: $r_s = -0.63$, $p = 0.0001$) and autochthonous species (N = 31; recorded: $r_s = -0.74$, $p < 0.001$; estimated: $r_s = -0.68$, $p < 0.0001$; Fig. 2), declining towards sites of higher connectivity. The correlations for the four connectivity periods were all of the same magnitude, since differences in lateral connectivity were marginal. Also when excluding Danube river sites correlations remained significant for all species (N = 27; recorded: $r_s = -0.63$, $p < 0.001$; estimated: $r_s = -0.54$, $p = 0.003$) and autochthonous species (N = 27; recorded: $r_s = -0.64$, $p < 0.001$; estimated: $r_s = -0.63$, $p = 0.0004$).

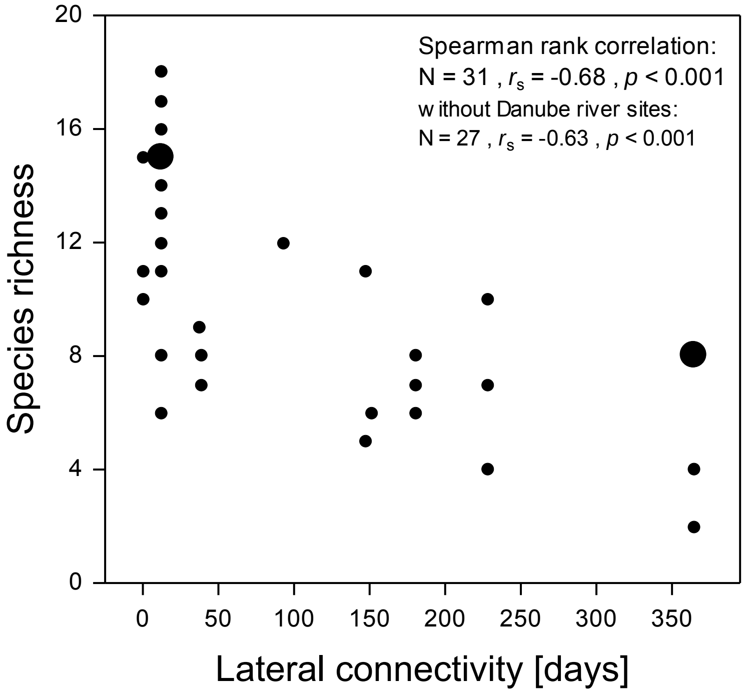

Figure 2: Relationship between estimated richness of autochthonous species and lateral connectivity. Larger bubbles indicate a larger number of sampling sites, Danube river sites are represented by the three dots on the right side of the graph.

Species richness was significantly positively influenced by habitat heterogeneity (HDI) when tested for all recorded species (ANOVA; $F_{3,27} = 7.5$, $p < 0.001$; without Danube river sites: $F_{3,23} = 4.57$, $p = 0.01$), estimated species ($F_{3,27} = 5.37$, $p = 0.005$; without Danube river sites: $F_{3,23} = 3.58$, $p = 0.03$), recorded autochthonous species ($F_{3,27} = 7.04$, $p = 0.001$; without Danube river sites: $F_{3,23} = 3.79$, $p = 0.02$), and estimated autochthonous species ($F_{3,27} = 5.34$, $p = 0.005$; without Danube river sites: $F_{3,23} = 3.26$, $p = 0.04$) (Fig. 3).

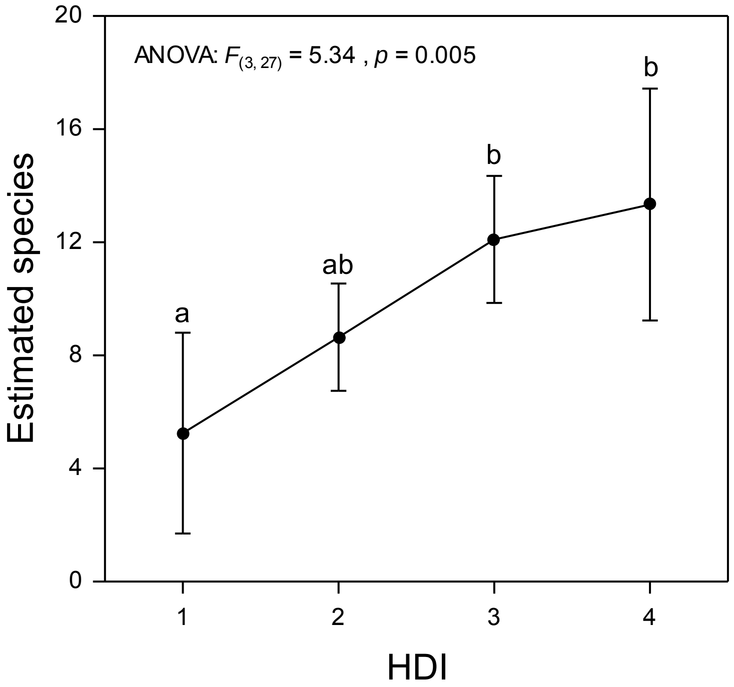

Figure 3: Mean estimated species richness (± 95% confidence intervals) depends on structural richness of habitat and rises with increasing HDI values. HDI = Habitat diversity index. Different letters above the whiskers indicate significant differences between means (Tukey's HSD post hoc tests).

Lateral connectivity did not differ significantly between HDI categories (Kruskal-Wallis test: $H_3 = 6.07$, $p = 0.11$) although a weak trend was visible that structurally more diverse habitats had a lower connectivity.

Relationships found by univariate tests between species richness and the environmental variables, lateral connectivity and HDI, were confirmed by the results of GLMs. The model including both variables explained 12-14% more of the variance in species richness than connectivity as single predictive variable. While habitat diversity had the least predictive power, the relationship with estimated richness was still significant (Tab. 2).

Table 2: Relationships between estimated species richness and habitat variables lateral connectivity and habitat diversity (HDI) tested with generalized linear models (GLM). Calculated models are ranked according to Akaike information criterion (AIC), which is a relative measure of the information content of statistical models.

Estimated richness	Variables included	AIC	Df	multiple r^2	p
All species	Connectivity, HDI	170.07	4	0.57	< 0.001
	Connectivity	174.37	1	0.43	< 0.001
	HDI	182.10	3	0.37	0.005
Autochthonous species	Connectivity, HDI	158.14	4	0.55	< 0.001
	Connectivity	160.79	1	0.43	< 0.001
	HDI	168.68	3	0.37	0.005

There was no clear effect of restoration status on all species (Kruskal-Wallis test; recorded: $H_2 = 5.10$, $p = 0.078$; estimated: $H_2 = 5.55$, $p = 0.062$). However, a significant effect of restoration status was indicated when excluding Danube river sites from the analyses (Kruskal-Wallis test; recorded: $H_2 = 11.13$, $p = 0.004$; estimated: $H_2 = 9.32$, $p = 0.01$), showing a decline of species at sites along side arms where restoration measures have been implemented. Autochthonous species showed a similar pattern: a non-significant tendency when including all sites (ANOVA; recorded: $F_{2,28} = 2.91$, $p = 0.071$; estimated: $F_{2,28} = 2.97$, $p = 0.067$), and a significant negative effect of restoration status on dragonfly species richness when excluding Danube river sites (ANOVA; recorded: $F_{2,24} = 7.84$, $p = 0.002$; $F_{2,24} = 6.84$, $p = 0.004$).

Abundance

Sightings of dragonflies were significantly related to lateral hydrological connectivity (for all sites: $r_s = -0.72$, $p < 0.001$; without Danube river sites: $r_s = -0.58$, $p = 0.002$). The number of counted individuals decreased with increasing connectivity (Fig. 4). Furthermore, dragonfly counts were significantly affected by HDI (ANOVA; all sites: $F_{2,28} = 3.18$, $p = 0.04$). More individuals were observed at sites characterized by a high HDI (Fig. 5).

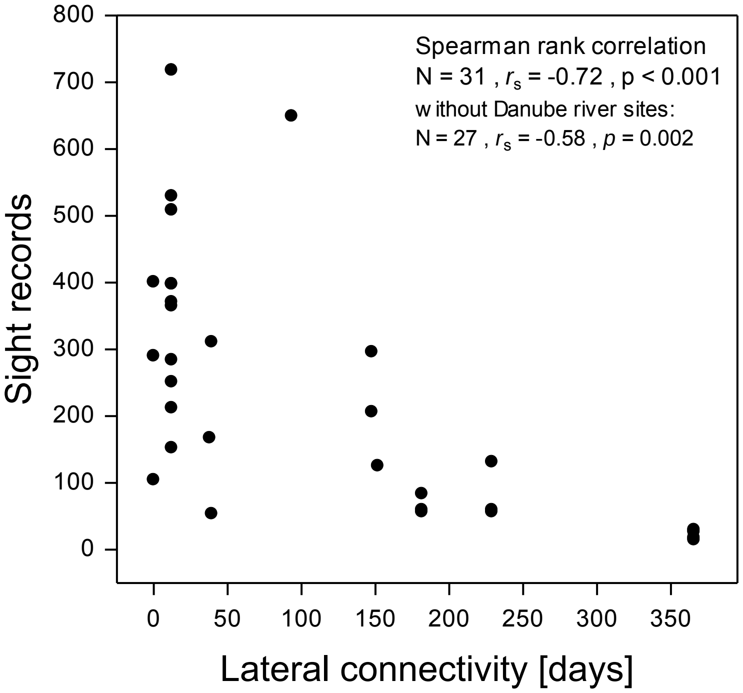

Figure 4: Relationship between number of recorded individuals and lateral connectivity. Danube river sites (connected 365da^{-1}) are represented by the dots on the right side of the graph.

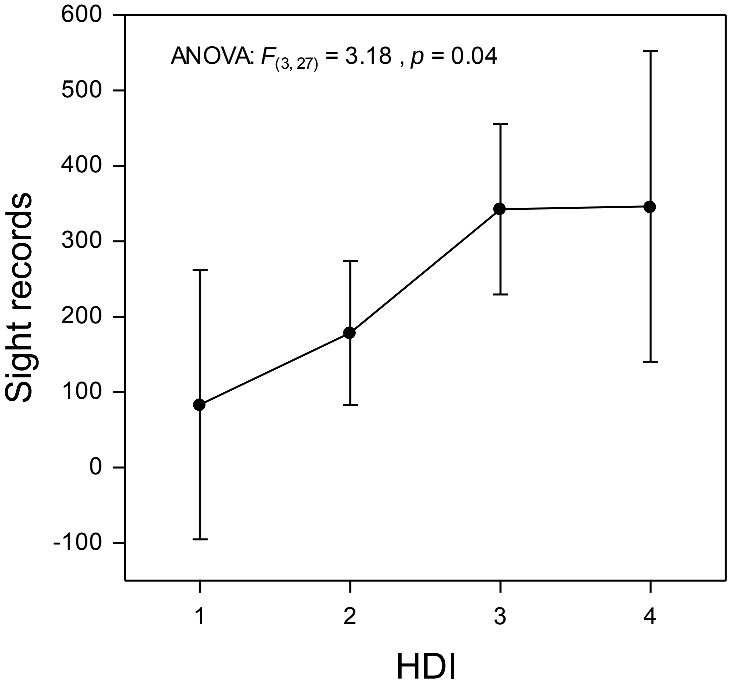

Figure 5: Mean number of recorded individuals (± 95% confidence intervals) increases with increasing habitat heterogeneity.

Faunal similarity

The NMDS plot based on Bray-Curtis similarities (Fig. 6) clearly visualizes that sites are grouped according to their lateral hydrological connectivity, forming two well separated groups of sites with lowest and highest connectivity, respectively, and interspersed by communities at sites of intermediate connectivity. The stress value (a measure of the poorness-of-fit of the representation of the original faunal distance matrix values by the ordination) of the two dimensional ordination was 0.1, indicating that this ordination was acceptable. While species composition differed significantly between all five groups of sites classified by their extent of lateral connectivity (one-way ANOSIM; all species: $r_{\mathrm{global}} = 0.65$, $p = 0.001$; autochthonous species: $r_{\mathrm{global}} = 0.64$, $p = 0.001$), no significant effect of HDI on composition of dragonfly assemblages was found (one-way ANOSIM: all species: $r_{\mathrm{global}} = 0.06$, $p = 0.18$; autochthonous species: $r_{\mathrm{global}} = 0.06$, $p = 0.16$). A two-way crossed ANOSIM (isolated and Danube river sites excluded due to low spatial replication) clearly indicated that side arms belonging to different connectivity categories (>0-30, >30.120, >120 da^{-1}) are characterized by distinct compositions of autochthonous species ($r_{\mathrm{global}} = 0.55$, $p = 0.001$). By contrast, HDI again did not significantly affect composition of dragonfly assemblages ($r_{\mathrm{global}} = 0.16$ $p = 0.12$). The corresponding pairwise comparisons of faunal similarities between groups of sites classified by connectivity illustrated significant differences between highly (>120 da^{-1}) and low connected sites (>0-30 da^{-1}) ($r = 0.76$, $p = 0.001$), but no significant differences between intermediate (>0-30 da^{-1}) and both low ($r = 0.28$, $p = 0.17$) and highly connected sites ($r = 0.53$, $p = 0.05$). The results of a two-way crossed ANOSIM including all recorded species did not substantially deviate from the relations found for autochthonous species. Furthermore, species composition was not affected by the status of river branch restoration (one-way ANOSIM; all species: $r_{\mathrm{global}} = 0.07$, $p = 0.18$; autochthonous species: $r_{\mathrm{global}} = 0.08$, $p = 0.17$).

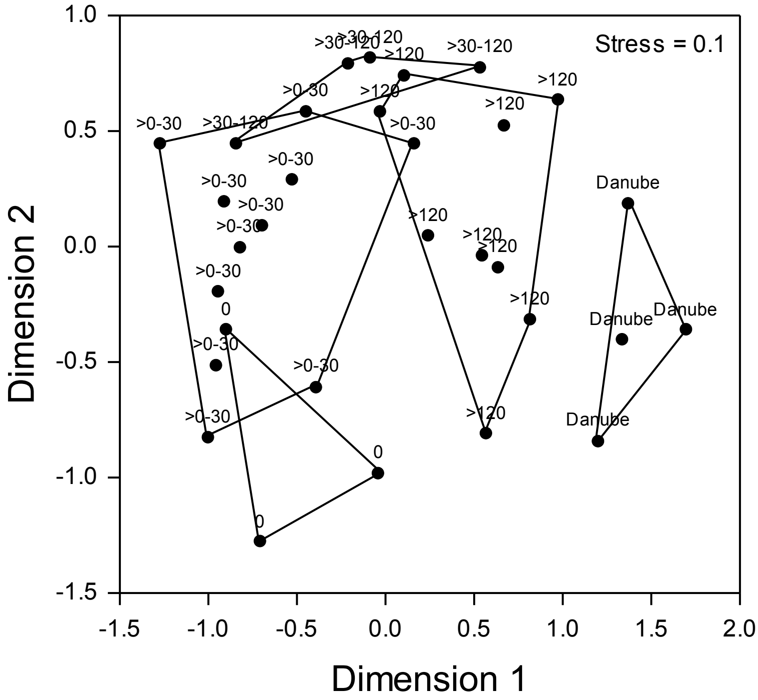

Figure 6: NMDS ordination of sites based on Bray-Curtis similarities. For better visualization, polygons connect sites grouped according to their lateral connectivity: (1) sites isolated from main stream, (2) sites connected for >0-30 da^{-1}, (3) for >30-120 da^{-1} and (4) >120 da^{-1}, and (5) Danube river sites.

Due to spatial autocorrelation of sites affecting species composition (Spearman matrix rank correlations; all species: *Rho* = 0.18, *p* = 0.005; autochthonous species: *Rho* = 0.18, *p* = 0.002), effects of habitat variables on species compositions were tested by partial Mantel tests, with geographical distances between sites as covariate.

While the effect of lateral connectivity on species composition was well-supported by partial Mantel tests (all species: *r* = -0.60, *p* < 0.001; autochthonous species: *r* = -0.59, *p* < 0.001; Fig. 7), also the comparison of Bray-Curtis similarities and differences of HDI between sites achieved significance when corrected for spatial autocorrelation (all species: *r* = -0.30, *p* < 0.001; autochthonous species: *r* = -0.30, *p* < 0.001). Yet, the effect of habitat diversity was distinctly weaker than the influence of lateral connectivity.

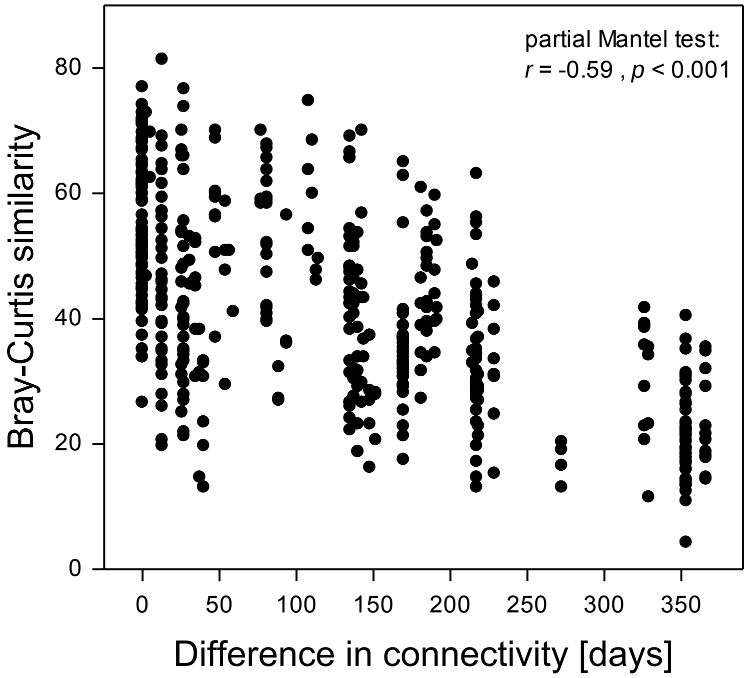

Figure 7: Relationship between faunal similarity (Bray-Curtis similarities) of autochthonous dragonflies and differences in lateral connectivity between sites. Similarity of communities strongly decreases if difference in duration of connectivity becomes greater.

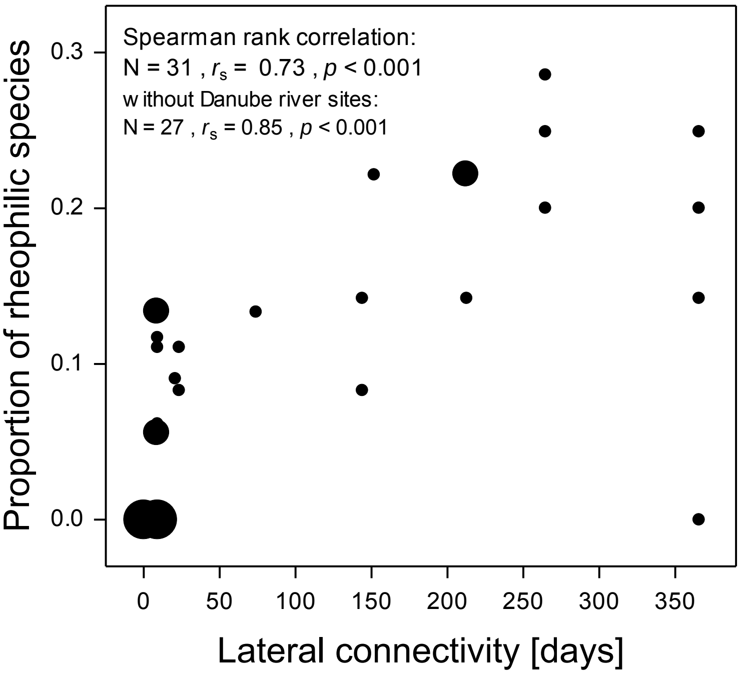

Figure 8: Relationship between proportion of rheophilic species and lateral connectivity. Larger bubbles indicate a larger number of sampling sites, Danube river sites are represented by the four dots on the right side of the graph.

Occurrence of rheophilic species

The proportion of recorded rheophilic species responded positively to lateral connectivity, irrespective of including all rheophilic species ($r_s = 0.73$, $p < 0.001$; without Danube river sites: $r_s = 0.85$, $p = 0.001$), or only rheophilic species classified as locally autochthonous ($r_s = 0.45$, $p = 0.01$; without Danube river sites: $r_s = 0.53$, $p = 0.005$) (Fig. 8).

HDI did not affect the proportion of rheophilic species, whether including Danube river sites (ANOVA; all rheophilic species: $F_{3,27} = 0.88$, $p = 0.47$; only autochthonous species: $F_{3,27} = 0.33$, $p = 0.80$) or excluding them from the analysis (ANOVA; all rheophilic species: $F_{3,23} = 0.61$, $p = 0.61$; only autochthonous species: $F_{3,23} = 0.34$, $p = 0.80$).

Proportion of rheophilic species changed significantly with restoration status when all recorded species were considered (ANOVA; $F_{3,28} = 10.85$, $p = 0.0003$; without Danube river sites: $F_{3,24} = 20.29$, $p < 0.0001$) and when only autochthonous species were included (Kruskal-Wallis test; $H_2 = 6.19$, $p = 0.045$; without Danube river sites: $H_2 = 7.04$, $p = 0.029$). The proportion of rheophilic species was higher at sites where restorations have been implemented, however did not differ between the two classes of restored sites.

Oviposition type

Recorded richness of dragonfly species with endophytic oviposition (Zygoptera and Aeshnidae) was significantly related to lateral connectivity for the entire species assemblage ($r_s = -0.78$, $p < 0.001$; without Danube river sites: $r_s = -0.69$, $p < 0.001$) and autochthonous species ($r_s = -0.76$, $p < 0.001$; without Danube river sites: $r_s = -0.65$, $p < 0.002$), decreasing towards highly connected sites. The number of recorded exophytic oviposing species did not respond significantly to stream connectivity ($r_s = -0.33$, $p = 0.067$; without Danube river sites: $r_s = -0.32$, $p = 0.1$), yet a negative trend was also apparent.

The number of recorded species with an endophytic oviposition mode was positively affected by HDI (ANOVA: $F_{3,27} = 5.22$, $p = 0.006$; without Danube river sites: $F_{3,23} = 3.31$, $p = 0.038$; autochthonous species: $F_{3,27} = 4.92$, $p = 0.007$; without Danube river sites: $F_{3,23} = 3.08$, $p = 0.048$). Number of species with exophytic oviposition did not always clearly respond to HDI (ANOVA: $F_{3,27} = 3.17$, $p = 0.04$; without Danube river sites: $F_{3,23} = 2.67$, $p = 0.071$; autochthonous species: $F_{3,27} = 2.82$, $p = 0.058$; without Danube river sites: $F_{3,23} = 1.94$, $p = 0.15$), but showed a positive tendency in all cases.

Discussion

Effects of connectivity, habitat diversity and restoration of river branches on dragonfly communities

This study showed that hydrological dynamics influenced species richness and composition of dragonfly communities in riverine floodplains, thereby paralleling patterns found across different other taxa (Bornette et al. 1998, Baranyi et al. 2002, Brunke 2002, Lasne et al. 2007). Increasing lateral connectivity reduced species richness and shaped community structure, a relation found in DFNP also for sponges (Dröscher & Waringer 2007) and molluscs (Reckendorfer et al. 2006).

Hydrological dynamics and the resulting lateral connectivity integrate a large set of habitat features such as stream velocity, hydraulic stress, nutrient input, sedimentation and macrophyte density (Tockner et al. 1999a, Amoros & Bornette 2002, Baranyi et al. 2002, Thoms 2003, Reckendorfer et al. 2006), thereby shaping habitat heterogeneity and bank structure. High lateral connectivity with strong flow events will lead to a more uniform bank structure along floodplain channels, while low connectivity will lead to a high rate of habitat senescence with the possibility that different types of structures can establish along channels. Although no significant relationship between lateral connectivity and habitat diversity was found in this study, a trend existed that strongly connected side arms had lower habitat diversity and sites isolated from the main river channel were more structured.

While dragonflies have been extensively used as qualitative bioindicators for the ecological integrity of Danube river-floodplain systems on different geographic scales (Chovanec & Waringer 2001, Chovanec et al. 2004), quantitative studies on changes of the local community structure as response to alteration of lateral hydrological connectivity and habitat diversity are surprisingly scarce. In the present study, dragonfly species richness and abundance proved to be strongly affected by lateral connectivity. Species richness was highest at sites with low hydrological connectivity (~9/12days) and at isolated channels and then continuously decreased with higher lateral connectivity. This corresponds to the findings of Chovanec et al. (2002) who found species richness to be higher in isolated man-made water bodies than in more connected ones in a nearby regulated section of the Danube. Tockner et al. (1999b) found highest richness at intermediate connectivity in a sub-section of the area sampled in the present study. Species richness patterns along environmental gradients (disturbance) often display peaks at intermediate states. For example, overall species richness of various invertebrate taxa can be highest in streams with intermediate frequency and intensity of bed movement (Townsend et al. 1997). In South African streams Stewart & Samways (1998) recorded a distribution of adult dragonflies corresponding to the predictions of the intermediate disturbance hypothesis. They found highest diversity in moderately disturbed and lowest diversity in highly disturbed rivers. However the response of single taxonomic groups may often deviate from this general pattern (Tockner et al. 1999b).

This study demonstrated that habitat diversity had a significant positive effect on species richness of dragonflies. Single species can have specific demands on habitats used for reproduction. While the occurrence of Zygoptera species depends on adequate vegetation structures for oviposition, open banks represent important perching sites for dragonflies of the family Gomphidae (Askew 2004). Consequently, a higher diversity of habitat structures favours coexistence of different ecological types, thereby increasing species richness. Habitat heterogeneity also proved to be of major importance for explaining species richness of dragonfly communities in ponds (Osborn & Samways 1996). Although structural diversity can promote the presence of a higher number of species, the occurrence of single species (e.g. of high conservation relevance) depends on the availability of specific habitat requisites such as open banks with gravel or sand for Gomphidae. The selection of suitable reproduction sites by dragonflies does not only depend on the reflection of polarized light from the aquatic surface (Wildermuth 1998) but is often proposed to be influenced by other structures of the water-land transition zone like bank vegetation and macrophytes (Corbet 1999, Askew 2004).

Time since the implementation of restoration measures considerably affected species richness of old Danube river branches. At sites without anthropogenically altered water dynamics species richness was higher than at sites where connectivity had been artificially enhanced. Because species richness and species composition did not differ significantly between sites restored in the years 1995 and 2002, respectively, dragonfly communities in the Danube floodplains appear to respond very fast to changes in lateral connectivity without a long lasting succession period characterized by a continuous species turnover.

Effects on dragonfly abundance

This study recorded that abundance of adult dragonflies decreased with increasing connectivity and decreasing habitat diversity. Higher hydrological connectivity filters the number of species capable to use such sites as habitats for reproduction. The small number of species tolerant to dynamic hydrological situations and the rarity of true rheophilic species in the study area (often characterized by low abundances; Raab 2000, Raab et al. 2006) may be important reasons for the lower abundances at sites with high lateral connectivity. Abundance can only be a rough proxy for biomass, especially as the difference in life weight of members of the two suborders can easily exceed the factor 50 (Askew 2004) but this should be outweighed by the generally low numbers of adult dragonflies at connected sites.

Abundance was also related to habitat diversity, a pattern that might be explained by the declining number of dragonfly species in more uniformly shaped habitats. Conversely, one might assume that effects of declining species richness might be compensated by the larger area of suitable habitats for species colonizing more homogeneously structured river stretches. The abundance of remaining species may also increase due to competitive release caused by a reduced interspecific competition. In fact, dependencies of dragonfly abundance on habitat structures have been reported (D'Amico et al. 2004, Butler & deMaynadier 2008) but the underlying reasons are not well understood. So far, increase of abundances of adult dragonflies in habitats with reduced habitat heterogeneity was only related to anthropogenic disturbance and reported exclusively for generalistic species (Clark & Samways 1996, Samways & Steytler 1996, Samways 2003), but not for habitat specialists adapted to colonize water bodies characterized by high hydrological dynamics.

Faunal similarity

Differences in lateral connectivity between study sites were reflected in faunal similarity. Species composition of dragonfly assemblages could be clearly distinguished between sites with low and high connectivity, while side arms with moderate connectivity were characterized by an odonate fauna intermediate between these two extremes. Hydrological dynamics also influence communities of zooplankton (Baranyi et al. 2002), aquatic plants (Bornette et al. 1998), aquatic invertebrates (Brunke 2002), sponges (Dröscher & Waringer 2007) and fishes (Lasne et al. 2007). The Austrian pool of dragonflies consists of a large number of species known from lentic habitats and many generalists able to colonize a wide range of aquatic habitats. Only a minority of species is restricted to running water (Raab et al. 2006). Therefore, in floodplain systems, where both types of water bodies are present, the structure of dragonfly assemblages strongly depends on the hydrological dynamics of individuals side arms.

Similarity of species composition was also related to the diversity of habitats in the sampled side arm section. Since habitat preferences of species vary, more species will be attracted by a higher structural diversity of habitats, but the species composition is affected by the colonization ability of individual species depending on the presence of particular habitat structures. Therefore, and because lateral connectivity itself is most likely shaping structural diversity of side arms (although the relationship did not achieve significance), the effect of habitat diversity on species composition was much weaker compared to the impact of lateral connectivity.

Rheophilic species

Three rheophilic species, *Calopteryx splendens*, *Gomphus vulgatissimus* and *Ophiogomphus celilia* (Askew 2004), were observed during this study. As expected, the proportion of rheophilic species increased with higher lateral connectivity. Qualitative investigations by Chovanec & Waringer (2001) and Chovanec et al. (2004) in sections of the Austrian Danube confirmed the occurrence of rheophilic dragonfly species particularly at side arms with higher connectivity. Also rheophilic species of sponges and molluscs are favoured by higher lateral connectivity of side arms (Dröscher & Waringer 2007, Reckendorfer et al. 2006). Not surprisingly, no effect of habitat diversity on the proportion of rheophilic species could be found, since these species do not particularly depend on different habitat types but specific structures such as open banks, which are typical for more uniformly-shaped sites with higher lateral connectivity. The effect of restoration status on rheophilic species most likely refers to differences in connectivity of sites, since sites restored in 2002 that showed a higher proportion of these species are connected for longer periods per year than sites restored in 1994.

Oviposition type

The number of species with endophytic oviposition decreased with lateral connectivity and increased with habitat diversity. Both results are likely to refer to the same phenomenon. Though Sahlén & Ekestubbe (2001) found no association between oviposition type and vascular plant richness, dragonfly species can have preferences for certain plant species as oviposition site (Gibbons et al. 2002). At channels with strong hydrological connection bank vegetation was more uniformly and aquatic macrophytes often were absent, whereas less connected channels had more diverse vegetation. Consequently, highly connected habitats should harbour fewer species with endophytic oviposition type.

Other filters for colonization

Many biotic and abiotic parameters can act as filters on the structure of dragonfly assemblages. Environmental conditions such as flow velocity, oxygen content, phosphate concentration, shade, aquatic vegetation (De Marco et al. 1999, Novelo-Gutiérrez et al. 2002, Hofmann & Mason 2005), presence of single plant species (Gibbons et al. 2002, Rantala et al. 2004), littoral vegetation (Butler & deMaynadier 2008), availability of specific microhabitats (Hawking & New 1999, Leipelt & Suhling 2001) and presence of predators (e.g. fishes; Johansson et al. 2006) are reported to significantly determine the distribution of larvae and adults.

While many studies suggested that odonate assemblages are chiefly structured by environmental (external) influences rather than biotic interactions (e.g. Osborn & Samways 1996), there are some authors that highlighted the importance of faunal interactions, e.g. intra- and interspecific competition (Mahato 2000, Hofmann & Mason 2005), and intraguild predation (Padeffke & Suhling 2003, Suutari et al. 2004), on densities of species and community composition. Such faunal interactions can strongly influence distribution and microhabitat choice of species, forcing them to occupy eventually suboptimal strata (Leipelt & Suhling 2001, Suutari et al. 2004, Hofmann & Mason 2005).

All these ecological parameters may have influenced patterns of species diversity and community similarities observed in this study and, therefore, should be kept in mind when interpreting these results. However, many of these abiotic and biotic variables are closely related or are direct consequences of the main driving force in floodplain systems, the hydrological dynamics. For example, important microhabitat variables such as aquatic vegetation or sediment quality (Lang et al. 2001) are both influenced by hydrological dynamics (Bornette et al. 1998).

The width of side arms and channels that were surveyed in this study differed and relations between size of water bodies and species richness have been found for dragonflies in ponds (Oertli et al. 2002). However, another study in DFNP has shown that surface area of water bodies had only a weak effect on dragonflies, which was clearly overridden by the effect of lateral hydrological connectivity (Tockner et al. 1999b).

Spatial autocorrelation in the data set of this study was a result of the roughly linear arrangement of sites along the main Danube river channel. Habitat isolation, recruitment limitation and dispersal ability can filter community structure (McCauley 2006). However, even small dragonfly species are able to disperse over wide distances (~ 2km) through suboptimal habitats (Rouquette & Thomson 2007) and tenerals (pre-reproductive adults) generally disperse from their molting sites to off-stream sites during maturation (Kirkton & Schultz 2001). The strong interconnection between channels of the river Danube floodplains and the resulting good accessibility for most species thus should promote fast colonization of habitats suitable for individual species. Even larger stretches of side arms with generally unfavourable conditions for individual species might offer some spatially limited refugia which at least can be used as stepping stones during dispersal but sometimes may even represent suitable habitat islands for reproduction. This is emphasized by the observation of males and females of the rheophilic species *Calopteryx splendens* displaying territorial behaviour where apertures in weirs allowed water flow at side channels otherwise characterized by low connectivity.

Implications for management

Historical sources report that before river regulation measures took place members of the families Gomphidae and Calopterygidae were important and abundant elements of the dragonfly fauna along the Austrian section of the Danube. These formerly common rheophilic species, which are indicators for lotic habitats, became rare due to river regulations (Schultz et al. 2003, Chovanec et al. 2004). Habitat specialists are more prone to local extinction than generalists (Korkeamäki & Suhonen 2002) and it was suggested that management should concentrate on the creation or maintenance of favourable conditions for lotic species (Hofmann & Mason 2005). Dragonflies were repeatedly used to describe the integrity of floodplain systems and to measure the success of river restoration programmes (Brunke 2002, Chovanec & Waringer 2001, Chovanec et al. 2004). However, other taxonomic groups do not necessarily have to respond in a similar manner. In fact, the impact of artificially altering lateral connectivity of side arms on diversity and community structure can be quite different (Tockner et al. 1999b, Amoros & Bornette 2002). Thus management planning has to evaluate cautiously the priorities of river and floodplain restoration schemes to achieve both aims, an increase of hydrological dynamics and the conservation of selected focus taxa.

Findings of this and other studies on dragonflies in floodplain systems documented that river restoration programs aiming to enhance connectivity of floodplain channels strongly affect dragonfly communities. If targeting to approach conditions resembling the historical situation of floodplains before river regulation, it is likely that rheophilic species of the families Gomphidae and Calopterygidae benefit from such implementations. At the same time, the realisation of such measures on large scales will negatively affect overall dragonfly species richness. The species loss may be reduced by maintaining individual river branches with low connectivity acting as refugia for odonates adapted to water bodies with low flow velocity. This also emphasizes that predictions of potential impacts of restoration measures should not only be based on individual taxa but have to consider a representative spectrum of taxonomic groups, as they may respond differentially.

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Appendix

Recorded species and number of observed individuals. Asterisks (*) indicate species that were not classified as autochthonous at respective sites. Sites are ranked according to their connectivity from low (left) to high (right) connectivity.

Species	Sites																
Suborder Zygoptera	s1	s14	s15	s6	s13	s16	s17	s18	s19	s22	s23	s26	s27	s30	s29	s24	s25
Family Calopterygidae																	
Calopteryx splendens (Harris, 1782)				1*		1*		1*		16	4		1*	2	3	1*	5
Family Lestidae																	
Chalcolestes viridis (Vander Linden, 1825)	4		1*	4	8	78	86		2				8	8			
Lestes sponsa (Hansemann, 1823)	8	1	5	1*	9		3						1*				
Sympecma fusca (Vander Linden, 1820)		27															
Family Coenagrionidae																	
Coenagrion hastulatum (Charpentier, 1825)	1*																
Coenagrion puella (Linnaeus, 1758)	42	5	38	62	60	33	30	20	11	2	61		107	57			
Erythromma najas (Hansemann, 1823)		2	141	57	75		2	45	54	30	7		71	20	2		
Erythromma viridulum (Charpentier, 1840)			10		20		30	30	50				30				
Ischnura elegans (Vander Linden, 1820)		3	41	7	12	18	48	62	173	60	26	11	84	40	18	5	21
Ischnura pumilio (Charpentier, 1825)													2		2		
Family Platycnemididae																	
Platycnemis pennipes (Pallas, 1771)	1*		24		11	6	59	125	291	185	95	93	86	78	112	24	242
Suborder Anisoptera																	
Family Gomphidae																	
Gomphus vulgatissimus (Linnaeus, 1758)				1*			1*			1*	2						
Ophiogomphus cecilia (Fourcroy, 1785)																	
Family Aeshnidae																	
Aeshna affinis Vander Linden, 1823	40	1*	2	1*	2	17	2		4	1*	1*		2	9		2	
Aeshna cyanea (Müller, 1764)	3			1*									1				1*
Aeshna grandis (Linnaeus, 1758)	23	3	6	21	11	2	5	3	2				2	1*			
Aeshna isosceles Müller, 1767)									1*								
Aeshna mixta Latreille, 1805	17	7	13	37	25		34	8	5	1*	3		2	7	2		1*
Anax imperator Leach, 1815			1*	4			1	2	6		3						1*
Anax parthenope Sélys, 1839							1*	2	3	3							
Family Corduliidae																	
Cordulia aenea (Linnaeus, 1758)			20	10	8		1*	16	17		7		1*				
Epitheca bimaculata (Charpentier, 1825)				6													
Somatochlora metallica (Vander Linden, 1825)		1*	5	2	2			1*	3	4	6			10	3	1*	2
Family Libellulidae																	
Crocothemis erythraea								1*	4								
Libellula depressa Linnaeus, 1758	2						1*					1*		1*			
Libellula quadrimaculata Linnaeus, 1758	3		2		3				1*								
Orthetrum albistylum (Sélys, 1841)									3					1		2	1*
Orthetrum cancellatum (Linnaeus, 1758)							29	21	21	20	7	8	2	4	7	6	6
Sympetrum meridionale (Sélys, 1841)	1*														1*		
Sympetrum pedemontanum (Allioni, 1766)										1*				4	1*		
Sympetrum sanguineum Müller, 1764)	116	43	44	10	70	35	112	56	49	21	24	10	87	67	18	2	11
Sympetrum striolatum (Charpentier, 1840)					3				20	5	2	10	2	51			15
Sympetrum vulgatum (Linnaeus, 1758)	30	14	50	59	80	24	87	7		15	3	21	22	11		13	5

Continued: Recorded species and number of observed individuals. Asterisks (*) indicate species that were not classified as autochthonous at respective sites. Sites are ranked according to their connectivity from low (left) to high (right) connectivity.

Species	Sites													
Suborder Zygoptera	s20	s9	s12	s11	s4	s5	s8	s2	s3	s7	s10a	s10b	s21	s28
Family Calopterygidae														
Calopteryx splendens (Harris, 1782)	220	51	5	37	1*	2	1*	3	16	1*		2		
Family Lestidae														
Chalcolestes viridis (Vander Linden, 1825)														
Lestes sponsa (Hansemann, 1823)														
Sympecma fusca (Vander Linden, 1820)						7				2				
Family Coenagrionidae														
Coenagrion hastulatum (Charpentier, 1825)														
Coenagrion puella (Linnaeus, 1758)	30	1*												
Erythromma najas (Hansemann, 1823)	32													
Erythromma viridulum (Charpentier, 1840)														
Ischnura elegans (Vander Linden, 1820)	132	54	20	1*	4		5	1*	3			1		
Ischnura pumilio (Charpentier, 1825)			5	8		2		3						
Family Platycnemididae														
Platycnemis pennipes (Pallas, 1771)	131	81	200	47	10		11	4	47	41	1*	2	1*	1*
Suborder Anisoptera														
Family Gomphidae														
Gomphus vulgatissimus (Linnaeus, 1758)	1*				1*			3	3	1*	1*			2
Ophiogomphus cecilia (Fourcroy, 1785)				1*		1*								1*
Family Aeshnidae														
Aeshna affinis Vander Linden, 1823	2		2				1							
Aeshna cyanea (Müller, 1764)												1*		
Aeshna grandis (Linnaeus, 1758)	1*								2					
Aeshna isosceles Müller, 1767)														
Aeshna mixta Latreille, 1805	7		1*		3	3		2	4					2
Anax imperator Leach, 1815														
Anax parthenope Sélys, 1839	2													
Family Corduliidae														
*Cordulia aenea (*Linnaeus, 1758)														
Epitheca bimaculata (Charpentier, 1825)														
Somatochlora metallica (Vander Linden, 1825)	3												2	
Family Libellulidae														
Crocothemis erythraea														
Libellula depressa Linnaeus, 1758														
Libellula quadrimaculata Linnaeus, 1758														
Orthetrum albistylum (Sélys, 1841)			1*											
*Orthetrum cancellatum (*Linnaeus, 1758)	1*	1*	9										3	
Sympetrum meridionale (Sélys, 1841)			6	4	2	1*			2	1*	1*	2	1*	6
Sympetrum pedemontanum (Allioni, 1766)	4		6											
Sympetrum sanguineum Müller, 1764)	75	8	14	13	5	37	18	11	19	4	4	8	14	12
Sympetrum striolatum (Charpentier, 1840)				1*	7	2	1*		4					3
*Sympetrum vulgatum (*Linnaeus, 1758)	9	12	28	16	26	31	23	35	33	7	9	2	6	4

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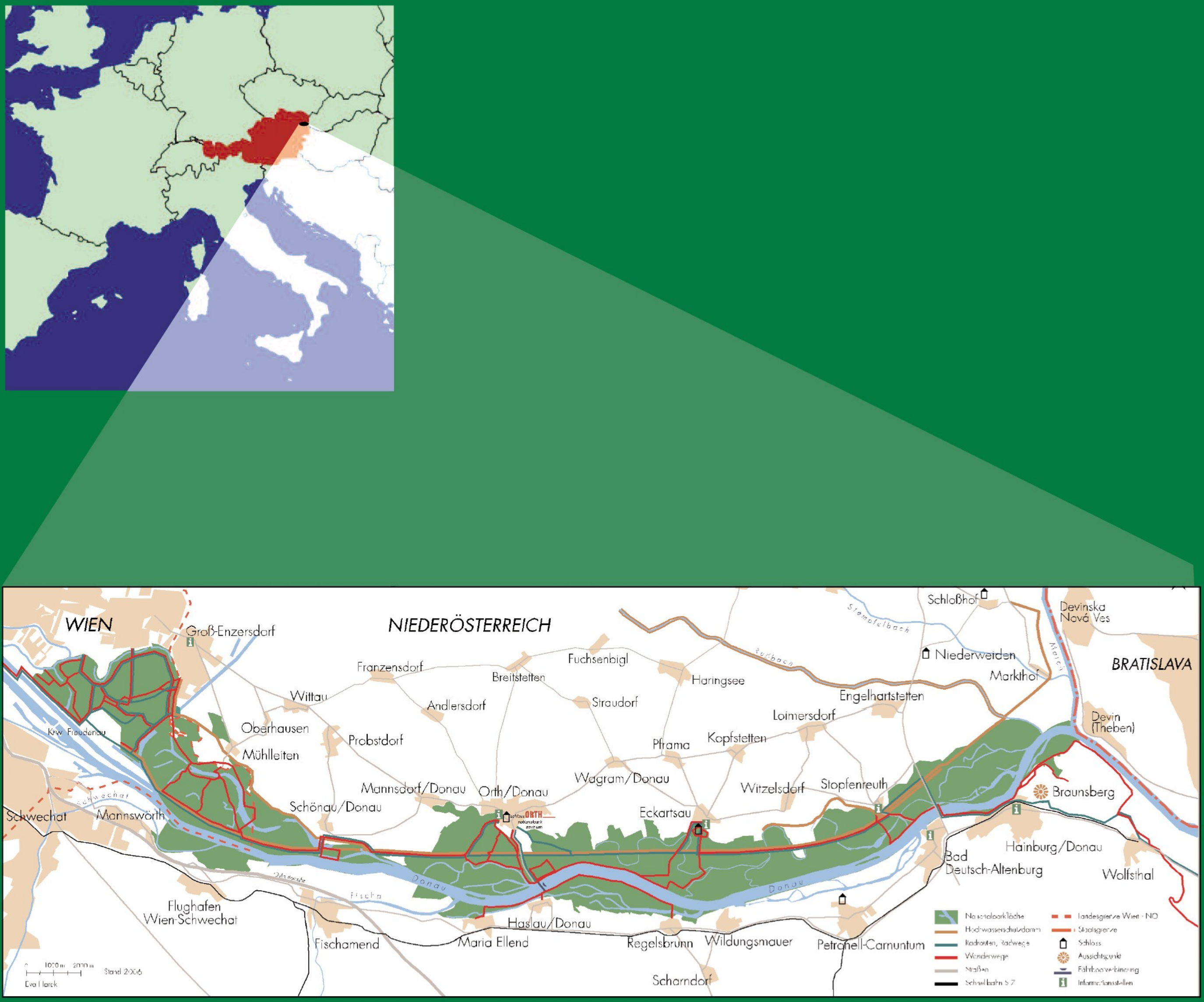

Nationalpark Donau-Auen GmbH
A-2304 Orth/Donau, Schloss Orth
Tel. 02212/3450, Fax DW 17
nationalpark@donauauen.at, www.donauauen.at

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