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Stormwater ponds promote dragonfly (Odonata) species richness and density in urban areas

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ABSTRACT

The loss of global biodiversity is one of the major challenges of our time and urbanisation is seen as a main cause of this. The aim of this study was to determine whether artificial stormwater ponds, designed to control water flow, can act as refuges for Odonata in urban areas. Moreover, we analysed the influence of habitat and landscape quality on dragonfly species richness and density of 35 stormwater ponds (STOPON) in comparison to 35 control ponds (CONTROL).

Our study revealed significant differences in environmental conditions between STOPON and CONTROL. At the habitat level, STOPON were larger, had a warmer microclimate, and lower concentrations of phosphate. STOPON were predominantly situated in suburbs, while CONTROL occurred mostly in rural areas. Accordingly, at the landscape level, STOPON had greater cover of built-up area as well as a lower cover of arable land and woodland. In line with this, the dragonfly assemblages at STOPON and CONTROL differed. Overall species richness was greater at STOPON than at CONTROL, and indicator species were only identified for STOPON. Especially threatened species benefited from STOPON, having higher species richness as well as higher adult and exuviae densities than CONTROL.

In conclusion, our study shows that stormwater ponds in urban areas play an important role in the conservation of dragonflies in general and threatened species in particular. At STOPON, as a result of regular management, the habitat quality was high and compensated for the low landscape quality stemming from significant urbanisation effects.

1. Introduction

For terrestrial biomes, land-use change is assumed to be the main cause of the recent biodiversity crisis (Sala et al., 2000). Worldwide, the greatest increase of a land-use type has been documented for urban areas (United Nations, 2010). Current scenarios assume a growth in the urban population from the present 3.5 billion to 6.3 billion in 2050. Urbanisation is a major reason for the extinction of species and for biotic homogenisation (McKinney, 2006; Grimm et al., 2008). Urbanisation leads directly to a loss of natural and semi-natural habitats (Balmford et al., 2003; McKinney, 2006; Steele and Heffernan, 2014). Indirectly, the fragmentation of the remaining habitat patches increases while the size of the habitats decreases (Lambin et al., 2001; Fahrig, 2003; Donnelly and Marzluff, 2006).

Water systems in cities are heavily modified, either for domestic and industrial use (Booth and Jackson, 1997; Paul and Meyer, 2001; Hassall, 2014; Hill et al., 2016) or for flood control (Hassall, 2014). In combination with a greater area of impervious surfaces through urbanisation, the hydrologic balance is disturbed and a higher magnitude of runoff as well as an increase in flood frequency are the results (Ehrenfeld, 2000; Steele and Heffernan, 2014).

To counteract the negative effects of urbanisation on the hydrologic balance, stormwater ponds have been constructed with increasing frequency over recent decades (Herrmann, 2012). Stormwater ponds are designed to mitigate runoff from impervious surfaces, as they are able to temporarily detain large amounts of water (Villareal et al., 2004; Gallagher, 2011).

A growing number of studies indicate that stormwater ponds not only fulfil a retention function but also attract aquatic and semi-aquatic species (Germany: Holtmann et al., 2017; USA: Birx-Raybuck et al., 2010; Canada: Hassall and Anderson, 2015; France: Scher and Thièry, 2005; Le Viol et al., 2009, 2012; Australia: Hamer et al., 2012).

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However, for Central Europe there are virtually no studies on the conservation value of stormwater ponds in urban areas.

Having a bipartite life cycle with aquatic and terrestrial stages, Odonata are good indicators of the habitat quality of both aquatic and terrestrial habitats (Sahlén and Ekestubbe, 2001; Foote and Hornung, 2005; Samways, 2008). As prominent predators and prey in a variety of aquatic and terrestrial habitats, they have a high ecological significance (Samways and Steytler, 1996; Knight et al., 2005). Due to their high dispersal ability, Odonata are able to colonize newly created habitats quickly (Corbet, 2004; Clausnitzer et al., 2009). In addition, their taxonomy and distribution are well known and sampling them with standard methods is manageable (D'Amico et al., 2004).

The aim of this study is to determine whether artificial stormwater ponds, designed to control water flow, can act as refuges for Odonata in urban areas. Moreover, we analyse the influence of habitat and landscape quality on dragonfly species richness and density in stormwater ponds in comparison to control ponds. Lastly, we develop recommendations for the management and construction of stormwater ponds as dragonfly habitats in urban areas.

2. Material and methods

2.1. Study area

The study area comprises the municipal area of the city of Münster (51°58″N, 7°38″E; 39–99 m a.s.l.) in the north of the German Federal State of North Rhine-Westphalia (Fig. 1). The city has about 305,000 inhabitants and covers an area of 303 km^2 (City of Münster, 2016). Of the total area, 34% consists of built-up and traffic areas; agricultural land covers 46%, forests 18% and bodies of water 2%. Biogeographically, the city is as a part of the Westphalian Basin located in the North German Plain. The climate is suboceanic with an annual precipitation of approximately 780 mm and a mean annual temperature of 9.9 °C (1981–2010; climate station Münster/Osnabrück; DWD, 2017).

Currently, 79 stormwater ponds exist in the study area (Möhring personal communication, Civil Engineering Office Münster). Their banks are usually not paved or concreted and all ponds are regularly managed to ensure a maximum volume of water retention. Management includes cutting of woody riparian plants and desludging of ponds every couple of years. The herb layer is usually cut every year, in the winter.

2.2. Sampling design

The study was conducted during the growing season in 2015. From the end of April to the beginning of September we investigated a total of 70 waterbodies, 35 stormwater ponds (STOPON) and 35 control ponds (CONTROL). A control pond was defined as the next pond in the vicinity of each STOPON (mean distance 781 m ± 99 m SE), regardless of whether it was man-made or of natural origin. Every pond was

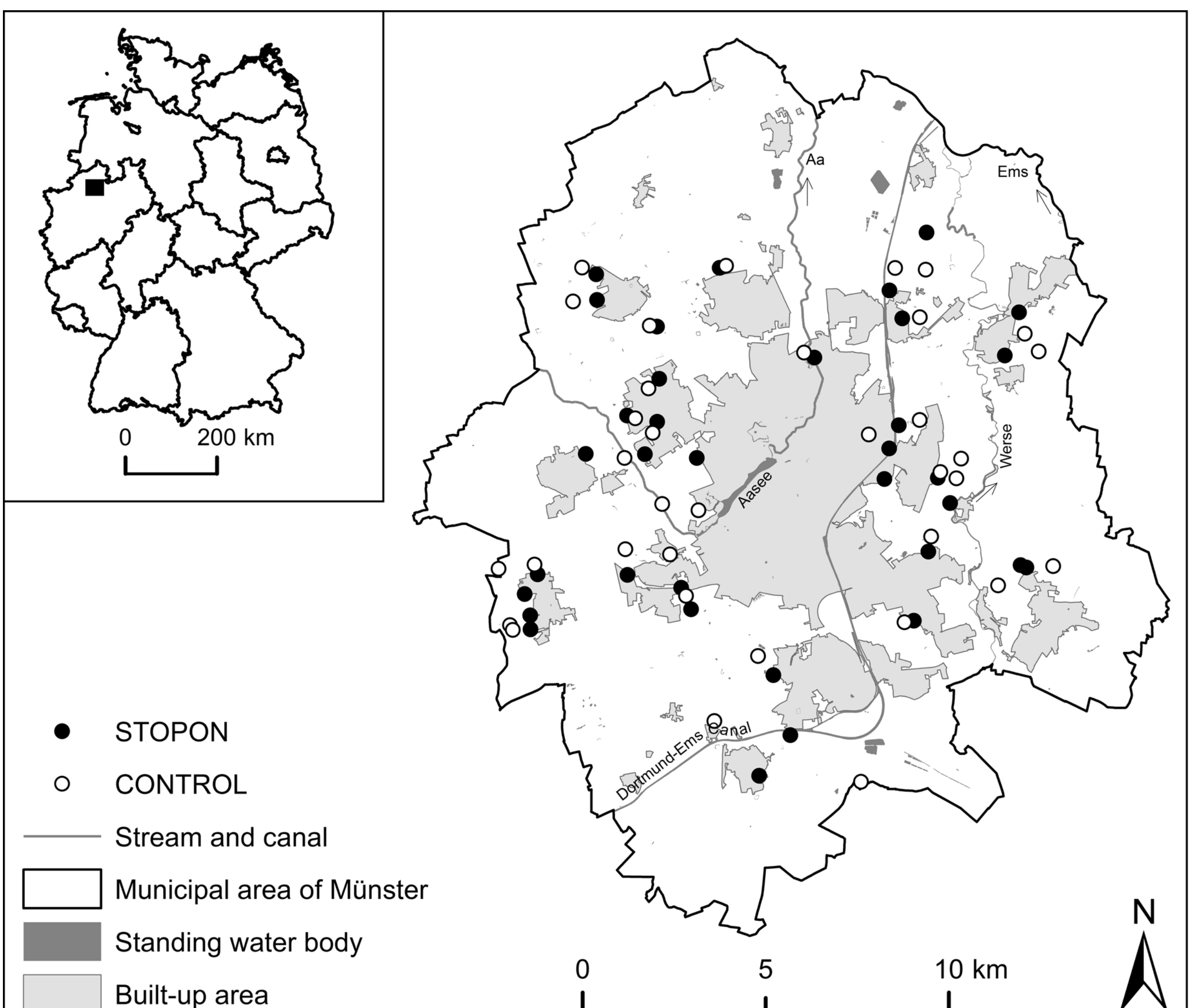

Fig. 1. Location of surveyed stormwater ponds (STOPON) and control ponds (CONTROL) in the municipal area of Münster (NW Germany). The inlay (upper left corner of the graph) shows the German Federal states and the location of the study area (black square) in Germany.

Table 1
Overview of sampled predictor parameters (mean ± standard error [SE], minimum and maximum). Differences between stormwater ponds (STOPON) and control ponds (CONTROL) were analysed by pairwise comparisons using paired *t*-test (*t*) or Wilcoxon test (*W*). Significant differences between the two pond types are indicated by bold type. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. = not significant.

Parameter	STOPON		CONTROL		P
	Mean ± SE	Min.–Max.	Mean ± SE	Min.–Max.	
Habitat level					
Structural parameters					
Size (m^2)[a]	2,369 ± 378	52–8,389	367 ± 130	18–3,390	***W******
Depth (cm)	34.9 ± 3.3	5–86	53.7 ± 5.4	5–136	***t*****
Hydrological parameters					
pH[b]	7.4 ± 0.0	6.8–8.3	7.3 ± 0.1	6.5–8.0	$W^{n.s.}$
Conductivity (µS/cm)[b]	592.3 ± 34.9	176–1,169	594.0 ± 42.6	165–1,403	$t^{n.s.}$
Water temperature (°C)[b]	23.9 ± 0.6	17.8–32.2	21.2 ± 0.6	15.0–28.5	***W****
Chloride (mg/l)[c]	29.9 ± 2.7	3.1–71.1	13.3 ± 1.4	0.0–40.0	***W******
Nitrite (mg/l)[c]	0.1 ± 0.0	0.0–0.5	0.0 ± 0.0	0.0–0.4	$W^{n.s.}$
Nitrate (mg/l)[c]	2.0 ± 0.5	0.0–9.5	1.0 ± 0.3	0.0–8.1	$W^{n.s.}$
Phosphate (mg/l)[c]	0.0 ± 0.0	0.0–1.0	0.3 ± 0.1	0.0–1.9	***W****
Ammonium (mg/l)[c]	0.7 ± 0.1	0.0–2.4	1.2 ± 0.3	0.0–5.7	$W^{n.s.}$
Potassium (mg/l)[c]	7.7 ± 1.1	1.0–29.9	6.1 ± 0.5	1.9–13.2	$W^{n.s.}$
Sodium (mg/l)[c]	21.2 ± 2.4	3.2–62.9	20.7 ± 9.5	2.9–324.1	***W*****
Vegetation cover (%)					
Open water surface	46.7 ± 6.4	0–100	62.6 ± 6.6	0–100	$t^{n.s.}$
Reed bed	35.4 ± 6.2	0–100	13.0 ± 3.6	0–75	***t*****
Algae	7.9 ± 3.6	0–100	5.2 ± 3.2	0–95	$W^{n.s.}$
Floating aquatic plants	9.0 ± 3.9	0–95	18.4 ± 5.9	0–100	$W^{n.s.}$
Submerged aquatic plants	5.7 ± 3.2	0–95	3.1 ± 1.8	0–55	$W^{n.s.}$
Riparian woodland	19.9 ± 4.1	0–80	49.6 ± 5.5	0–100	***t******
Daily sunshine duration (h)[d,e]					
August	7.9 ± 0.6	1.6–14.0	4.3 ± 0.6	0.0–13.0	***t******
Landscape level					
Land cover (%)[a]					
Grassland	9.3 ± 2.0	0–64	12.4 ± 1.8	0–58	$t^{n.s.}$
Woodland	11.0 ± 1.4	0–30	17.1 ± 2.4	2–55	***W****
Arable land	32.7 ± 3.0	0–63	45.3 ± 3.8	0–78	***W******
Built-up area	41.7 ± 2.8	5–75	22.0 ± 3.9	0–85	***W******
Urban green space	2.7 ± 0.9	0–24	1.6 ± 0.6	0–15	$W^{n.s.}$
Connectivity					
Distance to next three ponds (m)[a,f]	331.2 ± 29.2	92–952	266.4 ± 32.4	29–865	$t^{n.s.}$

[a] Calculated from aerial photographs by using ArcGIS 10.2.
[b] Measured by using a multi-parameter probe (Hanna HI 98129).
[c] Determined via ion chromatography.
[d] Measured by using a horizontoscope after Tonne (1954).
[e] Mean of four measures at N, E, S, W.
[f] Geometric mean.

investigated six times with a time lag of three weeks between each visit.

2.2.1. Habitat and landscape quality

For each waterbody, we sampled several environmental parameters (Tables 1 and 2). The pH, conductivity and water temperature were measured during each of the six visits. Prior to statistical analysis the data were pooled per parameter and pond. All other parameters that could not be derived from GIS calculations were recorded once between mid-July and mid-August. For spatial analyses, we used ArcGIS 10.2 and aerial photographs. For each pond, we calculated its size and its mean distance to the next three ponds (geometric mean) to quantify connectivity between ponds (Eichel and Fartmann, 2008; Poniatowski and Fartmann, 2010; Holtmann et al., 2017). Within a radius of 500 m around each pond we analysed landscape effects (Goertzen and Suhling, 2013; Jeanmougin et al., 2014). Furthermore, we took a water sample once in August at each pond and analysed it for anions and cations using an ion chromatograph (Metrohm, model 761 Compact IC).

Table 2
Absolute and relative frequencies of the categorical variables occurrence of fish and hydroperiod in stormwater ponds (STOPON) and control ponds (CONTROL). Differences in absolute frequencies between the two groups of ponds were analysed with the Chi-squared test. n.s. = not significant.

Parameter	STOPON		CONTROL		P
	N	%	N	%	
Fish					n.s.
Present	4	11.4	5	14.3	
Absent	31	88.6	30	85.7	
Hydroperiod					n.s.
Permanent	31	88.6	27	77.1	
Temporary	4	11.4	8	22.9	

2.2.2. Dragonfly assemblages

Raebel et al. (2010) recommend exuviae sampling as the best survey technique for Odonata. However, as Bried et al. (2012) demonstrated, Odonata sampling that is solely based on exuviae may lead to underestimations of species richness, especially concerning the presence of rare species. Consequently, in our study we used both adult and exuviae sampling during each of the six visits.

Since Odonata are poikilothermic organisms, we only recorded adults under favourable weather conditions (sunny and calm, minimum air temperature: 15 °C) and from 10 am to 6 pm (Sternberg and Buchwald, 1999). Adults were sampled with the help of a binocular for 15 min at standardised shoreline plots of 50 m^2 (25 m × 2 m). All

Table 3
Results of Indicator Species Analysis (ISA) () for stormwater ponds (STOPON) and control ponds (CONTROL) based on adult densities of autochthonous dragonfly species. Threat status (TS) in North Rhine-Westphalia after LANUV NRW (2010); faunal element (FE) after Sternberg (1998): Mediterranean (M) or Eurasian (E); IV = indicator value, ab = relative abundance comparing both pond types, % = frequency. Values in bold type: species are indicator species for this pond type. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. = not significant.

Species	TS	FE	IV	*P*	STOPON		CONTROL	
					ab	%	ab	%
Anisoptera								
Aeshna cyanea	.	E	18.1	n.s.	37	26	63	29
Aeshna mixta	.	M	8.9	n.s.	78	11	22	9
Anax imperator	.	M	17.6	n.s.	62	29	38	20
Brachytron pratense	x	E	2.9	n.s.	0	0	100	3
Cordulia aenea	.	E	5.7	n.s.	0	0	100	6
Crocothemis erythraea	.	M	1.4	n.s.	50	3	50	3
Libellula depressa	x	M	37.2	**	**81**	**46**	19	9
Libellula quadrimaculata	.	E	15.4	n.s.	67	23	33	17
Orthetrum brunneum	.	M	8.6	n.s.	100	9	0	0
Orthetrum cancellatum	.	M	22.4	*	**79**	**29**	21	11
Somatochlora metallica	.	E	2.9	n.s.	0	0	100	3
Sympetrum danae	x	E	2.9	n.s.	100	3	0	0
Sympetrum sanguineum	.	M	17.3	n.s.	55	31	45	26
Sympetrum striolatum	.	M	33.1	*	**72**	**46**	28	20
Zygoptera								
Chalcolestes viridis	.	M	18.3	n.s.	36	29	64	29
Coenagrion puella	.	M	32.7	n.s.	57	57	43	54
Enallagma cyathigerum	.	E	5.5	n.s.	48	11	52	9
Erythromma lindenii	.	M	8.6	n.s.	0	0	100	9
Erythromma najas	x	E	4.6	n.s.	81	6	19	9
Erythromma viridulum	.	M	19.1	n.s.	74	26	26	17
Ischnura elegans	.	E	48.4	**	**74**	**66**	26	31
Ischnura pumilio	x	M	17.1	*	**100**	**17**	0	0
Lestes dryas	x	E	2.9	n.s.	0	0	100	3
Platycnemis pennipes	.	E	6.1	n.s.	53	11	47	9
Pyrrhosoma nymphula	.	E	37.5	**	**77**	**49**	23	17
Sympecma fusca	.	M	2.9	n.s.	100	3	0	0

observed individuals within the plot were recorded and their species determined. If a determination was not possible, individuals were caught with a hand net, identified, and released immediately. Species were determined after Dijkstra and Lewington (2006).

Exuviae were sampled over an area of 10 m^2. Therefore, a ring of 1 m^2 size was randomly placed ten times around the shoreline. Within the ring, all exuviae were collected and determined in the lab using a digital microscope (Keyence digital microscope VHX-500FD, 20–200 times magnification) and the key of Brochard et al. (2012).

For all statistical analyses, only species autochthonous at a pond were considered. Species observed as exuviae and freshly hatched individuals were classified as autochthonous. Additionally, species with high adult abundance (total number of observed individuals: Zygoptera ≥ 10 individuals, Anisoptera ≥ 5 individuals, cf. Lohr, 2007) were also considered autochthonous. For statistical analyses of density data, we generally used the maximum value that was detected during one of the six visits.

For further analyses, dragonfly species were classified into threatened and not-threatened species according to the red data book of North Rhine-Westphalia (LANUV NRW, 2010). Moreover, we differentiated between Mediterranean and Eurasian species following Sternberg (1998) (Table 3). The different Mediterranean faunal elements (e.g., Atlanto-Mediterranean, Ponto-Mediterranean) were considered Mediterranean species, all other faunal elements (Ponto-Caspian, Siberian and Eurasian) having rather a continental distribution (cf. Sternberg, 1998) were considered Eurasian species (Willigalla and Fartmann, 2012).

2.3. Statistical analysis

As our study was based on a paired design, all sampled numerical parameters were tested for significant differences between STOPON and CONTROL by a paired *t*-test if the data were normally distributed; otherwise a Wilcoxon test was conducted. Differences in nominal variables were analysed using the Chi-square test. Differences in the explanatory power of habitat, landscape and synthesis models (see below [Fig. 3]) were analysed using repeated measures ANOVA with the Holm–Sidak test as a post hoc test.

Prior to multivariate analyses, Spearman rank correlations (r_s) were determined, in order to exclude variables with strong inter-correlations ($|r_s| \geq 0.6$). Nitrite was correlated with nitrate ($r_s = 0.80$, $P < 0.001$), sodium with chloride ($r_s = 0.79$, $P < 0.001$), sunshine duration in August with water temperature ($r_s = 0.69$, $P < 0.001$) and riparian woodland ($r_s = -0.60$, $P < 0.001$) as well as arable land with built-up area ($r_s = -0.75$, $P < 0.001$). Consequently, nitrite, sodium, sunshine duration, and arable land were excluded from the analyses described below. Accordingly, all remaining parameters in Tables 1 and 2 were included.

To evaluate the influence of habitat and landscape quality on species richness and density at STOPON and CONTROL separately, we applied Generalized Linear Models (GLM). At the habitat level, we conducted a GLM for each environmental parameter separately (Appendix A) to reduce the number of predictor variables and to avoid an over-fitting (Dormann et al., 2013). Only significant parameters were integrated into the habitat model. At the landscape level, the number of predictor variables was much lower and all variables could be integrated into the model. Finally, all significant variables of the habitat and landscape model were incorporated in a synthesis model (Table 4). Non-significant parameters were excluded by stepwise backward selection (step-function). We chose a stepwise procedure based on AIC, as it usually produces sound results and is widely used by scientists (Schröder et al., 2009; Thiele and Markussen, 2012). The use of a multi-model approach was discarded, because different models may fit the data approximately equally well and model selection may therefore be uncertain (Whittingham et al., 2006).

Subsequently, we tested each GLM for spatial autocorrelation in the residuals by calculating Global Moran's I (R package: lctools; Kalogirou 2017). Since there were no significant results ($P > 0.05$), statistical bias in our analyses due to spatial autocorrelation was rejected (cf. Diniz-Filho et al., 2003).

To identify indicator species for each pond type, an indicator species analysis (ISA) (Dufrêne and Legendre, 1997) was carried out. The analyses were performed using PC-ORD 5 (MjM Software Design, Gleneden Beach, OR, US), R-3.4.1 (R Development Core Team, 2017), SigmaPlot 13.0 and IBM SPSS Statistics 23.

3. Results

3.1. Environmental parameters

Many environmental parameters differed significantly between the two pond types (Table 1). At the habitat level, STOPON were larger and had a higher cover of reed beds than CONTROL. Additionally, they had higher concentrations of chloride and sodium but lower concentrations of phosphate. The lower cover of riparian woodland at STOPON results in higher sunshine duration (cf. the inter-correlations in the statistical analysis section, Section 2.3). Together with the fact that these water bodies are shallower, it provokes higher water temperatures in STOPON than in CONTROL (cf. the inter-correlations in the statistical analysis section, Section 2.3). The remaining numerical parameters did not differ between the two pond types.

The vast majority of the studied ponds were permanent ponds without fish ($N = 49$, 70%) (Table 2). Neither the presence of fish nor the hydroperiod differed between STOPON and CONTROL.

Table 4

Statistics of GLM (synthesis models): Relationship between species number (a), adult density (b), exuviae density (c) and environmental parameters of stormwater ponds (STOPON) and control ponds (CONTROL). Non-significant parameters were excluded by stepwise backward selection by AIC values (step function). In all models, the significance of the predictors was assessed using likelihood ratio tests. Differences between the levels of the intercepts were analysed using Wald tests. All models were calculated using Poisson error structure, or negative-binomial error structure in case of overdispersion. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. = not significant, R^2_{MF} = Pseudo-R^2 [McFadden].

STOPON				CONTROL			
Parameter	Estimate	SE	P	Parameter	Estimate	SE	P
a) Species richness							
Threatened species (R^2_{MF} = 0.13)				*Threatened species* (R^2_{MF} = 0.35)			
Intercept	−3.415	1.551	*	Intercept	−0.728	0.599	n.s.
Water temperature	0.125	0.061	*	Riparian woodland	−0.029	0.016	*
Mediterranean species (R^2_{MF} = 0.29)				*Mediterranean species* (R^2_{MF} = 0.52)			
Intercept	2.077	0.212	***	Intercept	1.892	0.183	***
Built-up area	−0.023	0.005	***	Phosphate	−1.188	0.581	*
				Ammonium	−0.375	0.163	**
				Riparian woodland	−0.018	0.005	***
Eurasian species (R^2_{MF} = 0.22)				*Eurasian species* (R^2_{MF} = 0.25)			
Intercept	1.443	0.283	***	Intercept	0.165	0.250	n.s.
Built-up area	−0.020	0.007	**	Built-up area	−0.019	0.010	*
				Size	0.001	0.000	***
b) Adult density (individuals/10 m²)							
Threatened species (R^2_{MF} = 0.53)				*Threatened species* (R^2_{MF} = 0.42)			
Intercept	1.084	0.823	n.s.	Intercept	−3.256	0.863	***
Distance to next three ponds	−0.004	0.002	*	Submerged vegetation	0.065	0.023	*
Built-up area	−0.037	0.015	*				
Algae	0.029	0.008	**				
Size	0.000	0.000	***				
Mediterranean species (R^2_{MF} = 0.17)				*Mediterranean species* (R^2_{MF} = 0.31)			
Intercept	3.087	0.536	***	Intercept	2.611	0.408	***
Built-up area	−0.035	0.012	**	Riparian woodland	−0.025	0.007	***
				Built-up area	−0.023	0.011	*
Eurasian species (R^2_{MF} = 0.39)				*Eurasian species* (R^2_{MF} = 0.30)			
Intercept	1.734	0.444	***	Intercept	0.981	0.209	***
Built-up area	−0.018	0.007	**	Ammonium	−1.492	0.445	***
Woodland	0.044	0.014	**				
Distance to next three ponds	−0.002	0.001	***				
c) Exuviae density (individuals/10 m²)							
Threatened species (R^2_{MF} = 0.50)				*Threatened species* (R^2_{MF} = 0.30)			
Intercept	−0.272	0.695	n.s.	Intercept)	−0.328	0.551	n.s.
Size	0.000	0.000	**	Riparian woodland	−0.042	0.020	**
Depth	0.022	0.007	**				
Riparian woodland	−0.019	0.008	**				
Mediterranean species (R^2_{MF} = 0.41)				*Mediterranean species* (R^2_{MF} = 0.38)			
Intercept	0.319	0.454	n.s.	Intercept	3.025	0.413	***
Woodland	0.073	0.027	*	Phosphate	−3.155	0.927	***
				Built-up area	−0.041	0.013	**
Eurasian species (R^2_{MF} = 0.31)				*Eurasian species* (R^2_{MF} = 0.50)			
Intercept	3.147	0.496	***	Intercept	0.976	0.528	n.s.
Built-up area	−0.042	0.011	***	Phosphate	−2.046	0.950	*
				Built-up area	−0.039	0.017	*
				Size	0.001	0.000	**

STOPON were predominantly situated in the suburbs, while CONTROL were mostly located in rural areas (Fig. 1). Accordingly, at the landscape level, the cover of the built-up area was greater in the surroundings of STOPON but the cover of woodland and arable land were higher around CONTROL (Table 1). The other numerical parameters, including connectivity, did not differ between the two pond types.

3.2. Dragonfly assemblages

3.2.1. Species richness and density

We recorded a total of 26 autochthonous dragonfly species (14 Anisoptera, 12 Zygoptera) at the 70 waterbodies, 21 at STOPON and 22 at CONTROL (Table 3). About half of the species were Mediterranean (46%) and half Eurasian (54%). Six of the species are considered threatened in North Rhine-Westphalia. At STOPON, the most frequent species was *Ischnura elegans,* occurring at 23 ponds (66% of all stormwater ponds), followed by *Coenagrion puella*, found at 20 ponds (57%). At CONTROL, *C. puella* was the most widespread species, appearing at 19 ponds (54%).

The ISA identified six indicator species for STOPON: *I. elegans*, *Ischnura pumilio, Libellula depressa*, *Orthetrum cancellatum, Pyrrhosoma nymphula* and *Sympetrum striolatum*. Two of these indicator species are considered threatened (*I. pumilio* and *L. depressa*). In contrast, CONTROL had no indicator species.

Overall species richness was significantly greater at STOPON

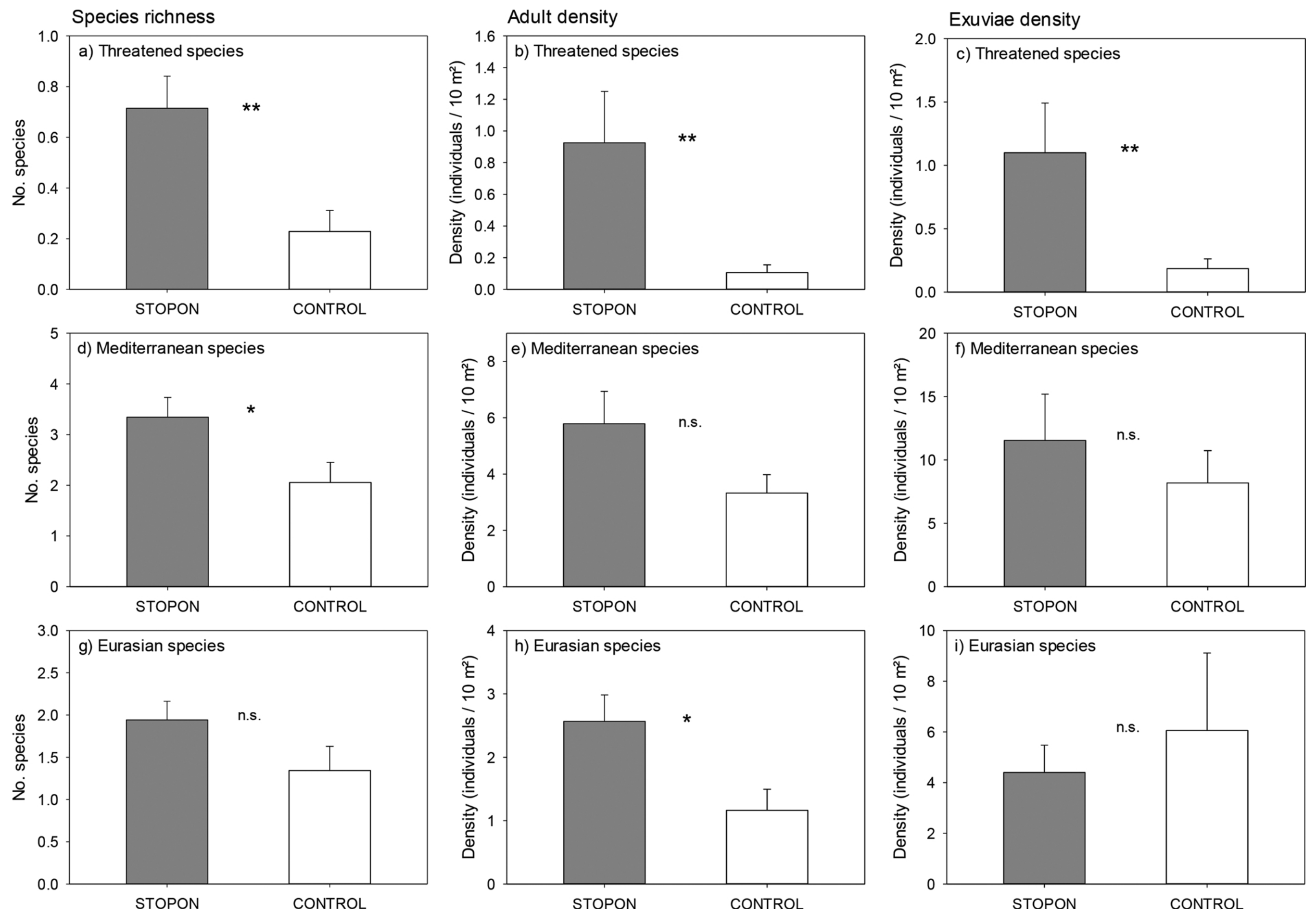

Fig. 2. Mean (± SE) number of species (a, d and g), adult density (b, e and h), and exuviae density (c, f and i) of dragonflies in stormwater ponds (STOPON) and control ponds (CONTROL). Differences between the two pond types were tested using paired *t*-test for Eurasian species, all others were tested by Wilcoxon test. * $P < 0.05$, ** $P < 0.01$, n.s. not significant.

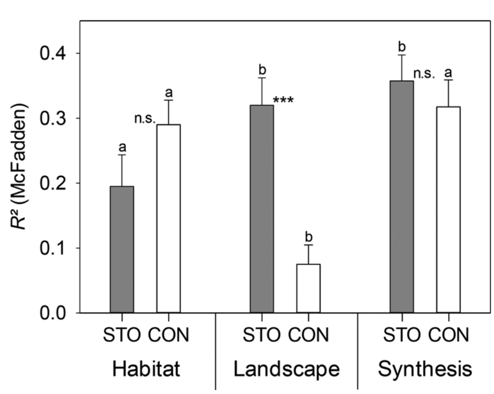

Fig. 3. Mean (± SE) R^2 values (McFadden) of habitat ($N = 18$), landscape ($N = 18$) and synthesis models ($N = 18$) (cf. Appendix A) for stormwater ponds (STO) and control ponds (CON). Differences between the two pond types were tested using paired *t*-test. *** $P < 0.001$, n.s. not significant. Differences between model types were analysed using repeated measures ANOVA with Holm–Sidak test as a post hoc test. STO: ANOVA, $F = 7.143$, $df = 2$, $P < 0.01$; CON: ANOVA, $F = 21.793$, $df = 2$, $P < 0.001$. Different letters indicate significant differences between groups (Holm–Sidak test, $P < 0.05$).

(5.3 ± 0.6) than at CONTROL: (3.4 ± 0.7) (paired *t*-test, $t = 2.4$, df = 34, $P < 0.05$). For threatened species, all three response variables (species richness, adult density, and exuviae density) had significantly higher values at STOPON compared to CONTROL (Fig. 2). In contrast, in Mediterranean species, only the number of species and, in Eurasian species, only the density of adults, were significantly higher at STOPON.

3.2.2. *Response of dragonfly assemblages to habitat and landscape quality*

Habitat and landscape quality determined dragonfly species richness and density (Table 4). However, the relevance of both to dragonfly assemblages differed between STOPON and CONTROL (Fig. 3). At STOPON, the habitat models had the lowest explanatory power (R^2 McFadden) significantly differing from the landscape and synthesis models. In contrast, at CONTROL, the model accuracy was lowest for the landscape models, significantly differing from those of the two other model types. Accordingly, despite the similarly high explanatory power of the habitat and synthesis models between STOPON and CONTROL, at STOPON, the model accuracy was significantly higher in the landscape models compared to CONTROL.

At the habitat scale, dragonfly assemblages were especially influenced by microclimate, the concentration of nutrients (ammonium, phosphate), and waterbody size (Table 4). In 6 of the 18 models, parameters associated with a warm microclimate (low cover of riparian woodland [cf. inter-correlations in Section 2.3], high water temperature) favoured the richness and density of threatened species as well as of Mediterranean species. This was especially the case at CONTROL, as it has a higher cover of riparian woodland (cf. Table 1). A negative effect of high ammonium and phosphate concentrations on species richness and dragonfly density was only observed at CONTROL (Table 4). In contrast, the size of the waterbodies had a positive effect on species richness and density of dragonflies at both pond types.

Additional parameters with positive effects on the density of threatened species in one model were cover of algae, cover of submerged vegetation, and waterbody depth.

At the landscape scale, the parameters associated with urbanisation had the greatest influence on dragonfly assemblages. The cover of built-up area in the surrounding of the ponds had negative effects on species richness and density in the majority of the models (10 of 18 models). Additionally, a higher cover of woodland, a rare biotope in the surrounding of the stormwater ponds (Table 1), and pond connectivity promoted dragonfly density in two of the models in each case.

4. Discussion

Our study revealed significant differences in environmental conditions between STOPON and CONTROL (cf. Holtmann et al., 2017). At the habitat level, STOPON were larger, had a warmer microclimate, and lower concentrations of phosphate. STOPON were predominantly situated in suburbs, while CONTROL occurred mostly in rural areas. Accordingly, at the landscape level, STOPON had a greater cover of built-up area as well as a lower cover of arable land and woodland. In line with this and, in contrast to previous findings on amphibian assemblages from the same study area (Holtmann et al., 2017), dragonfly assemblages differed strongly between STOPON and CONTROL. Overall species richness was greater at STOPON than at CONTROL and indicator species were only identified for STOPON. Especially threatened species benefited from STOPON, having higher species richness as well as higher adult and exuviae densities compared to CONTROL.

According to Menke & Göcking (Münster Dragonfly Working Group, personal communication) 34 dragonfly species are currently autochthonous in the city of Münster. With *Orthetrum brunneum* and *Sympetrum danae*, we confirmed reproduction for two additional species in the city area. Consequently, with 21 autochthonous dragonfly species, STOPON harboured about 58% of the total dragonfly fauna of the 36 species of the city of Münster. A previous study from Münster (Willigalla et al., 2003) and studies from some Central European cities (Meier and Zucchi, 2000; Willigalla and Fartmann, 2009) detected similar numbers at stormwater ponds: 19 to 22 autochthonous dragonfly species.

Urban stormwater ponds not only host many different dragonfly species, the dragonfly assemblages of STOPON also had a higher mean species richness and density than CONTROL. This was especially true for threatened species. Additionally, indicator species, among them the two threatened species *I. pumilio* and *L. depressa*, were only identified for STOPON. This is in line with other studies, which have shown that stormwater ponds can act as important habitats for rare dragonfly pioneer species (Willigalla et al., 2003; Ott 2008; Willigalla and Fartmann, 2009, 2012). In contrast, the species-poor dragonfly assemblages of CONTROL were almost completely formed by widespread habitat generalists.

We assume that the high importance of the studied stormwater ponds for dragonflies in general and threatened species in particular was the result of a high habitat quality due to the regular management of the ponds. This assumption corroborates findings of a previous study from the same study area, showing that stormwater ponds had a higher habitat quality than ponds in the surrounding landscape, and that this had beneficial effects on amphibians (Holtmann et al., 2017).

Stormwater pond management in the study area includes cutting of woody riparian plants and desludging every couple of years together with mowing of the herb layer, usually every year during the winter (cf. Section 2.1, 'Study area'). Consequently, in contrast to CONTROL, STOPON had a very low cover of riparian woodland ($\sim$20%) leading to high sunshine duration, which, together with the shallowness of these water bodies, results in high temperatures in both the ponds and the adjacent terrestrial habitats (cf. inter-correlations in Section 2.3 as well as Stoutjesdijk and Barkman, 1992). Additionally, due to the regular plant removal and desludging, the nutrient concentrations were generally relatively low and phosphate concentrations were even lower than at CONTROL.

Dragonflies have a tropical origin (Pritchard and Leggott, 1987; Corbet, 2004). Accordingly, diversity increases with temperature from the poles to the equator, except in regions with low precipitation (Kalkman et al., 2008). In Central Europe, however, water is widely available and summer temperatures seldom exceed 30 °C (Ellenberg and Leuschner, 2010). Hence, temperature is here the main limiting factor in general and in particular for Mediterranean species (Sternberg and Buchwald, 1999; Willigalla and Fartmann, 2012). In line with this, a cooler microclimate due to shading (cf. Hassall et al., 2011; Jeanmougin et al., 2014) was the main factor limiting species richness and density of threatened and Mediterranean species at CONTROL, but only partly at STOPON.

Additionally, we detected negative effects of ammonium and phosphate concentrations on species richness and density of dragonflies at CONTROL. As hydrochemistry only plays a subordinate role for dragonflies (Schlüpmann, 1995; Sternberg and Buchwald, 1999; Beketov, 2002) and ammonium and phosphate concentrations were not extremely high (maximum: 5.7 and 1.9 mg/l, respectively) (cf. Pott and Remy, 2000) we exclude a direct negative effect of these nutrients. On the contrary, we assume again that the genuine effect underlying this relationship was a cool microclimate. On average, 50% of the shoreline of CONTROL was covered by riparian woodland, resulting in low sunshine duration and a cool microclimate together with a nutrient-enrichment due to leaf accumulation in the mostly unmanaged water bodies (own observation). Indeed, at CONTROL, ammonium and phosphate concentrations were significantly negatively correlated with sunshine duration in August ($r_s = -0.46, P < 0.01$ for ammonium and $-0.37, P < 0.05$ for phosphate).

Several studies have shown that species richness rises with increasing habitat size (Field et al., 2009), as it is a substitute for habitat heterogeneity (Steinmann et al., 2011). This is also true for dragonflies (Oertli et al., 2002; Kadoya et al., 2004; Jeanmougin et al., 2014). Indeed, habitat size was also a driver of dragonfly species richness and density in our study. The majority of the studied stormwater and control ponds were small and poorly vegetated (cf. Table 1). Accordingly, factors that increase habitat heterogeneity and resource availability (cover of algae, cover of submerged vegetation, and pond depth) within the ponds also favoured dragonfly assemblages (cf. Foote and Hornung, 2005; Goertzen and Suhling, 2013; Jeanmougin et al., 2014; Holtmann et al., 2017).

At the landscape scale, STOPON were predominantly situated in the suburbs. Consequently, parameters associated with urbanisation had strong negative effects on dragonfly assemblages. Among these parameters, the most important one was the cover of built-up area in the surroundings of the ponds (cf. Jeanmougin et al., 2014). A high amount of built-up areas implies the direct loss of natural and semi-natural habitats for wildlife (Villalobos-Jiménez et al., 2016). Indirectly, landscape fragmentation increases and the remaining habitat patches become isolated (Hamer and McDonnell, 2008). Though not achieving cover values as high as in the surrounding of STOPON, built-up areas also had negative effects on dragonfly species richness and density in some of the CONTROL models.

In contrast, the cover of woodland in the surrounding of STOPON had positive effects on dragonfly density. Woodlands can act as dispersal corridors and terrestrial habitats for foraging and thermoregulation (Kuhn and Burbach, 1998; Kadoya et al., 2008), especially if forests are light and rich in forest glades, as was mostly the case in our study area (own observation). Samways and Steytler (1996) and Jeanmougin et al. (2014) also underlined the importance of forests for Odonata in urban landscapes.

Besides sufficient suitable terrestrial habitats and movement corridors, pond connectivity is also important for dragonflies (Kuhn and Burbach, 1998; Corbet, 2004), especially in highly fragmented landscapes such as urban areas. In line with this, at STOPON, adult dragonfly densities decreased with increasing distance between the ponds.

In conclusion, our study shows that in urban areas stormwater ponds play an important role for the conservation of dragonflies in general and threatened species in particular. At STOPON, as a result of regular management, the habitat quality (early successional stages, warm microclimate) was high and compensated for the low landscape quality due to strong urbanisation effects (high cover of built-up areas, low pond connectivity). In contrast, CONTROL, despite its much higher landscape quality, had species-poor dragonfly assemblages. This is very likely the result of a low habitat quality due to a lack of pond management.

5. Implications for conservation

This study illustrates the great importance of stormwater ponds for dragonfly conservation in urban areas, especially due to their relatively high habitat quality as a result of regular pond management. However, the construction and management of stormwater ponds can still be optimised and should focus on both the habitat and the landscape level.

At the habitat level, vegetation heterogeneity within the water bodies can be enhanced if cutting the aquatic vegetation and desludging is performed in a mosaic-like manner from year to year and not, as currently applied, to the whole stormwater pond at once (Holtmann et al., 2017). Additionally, at less sunlit ponds, shading woody plants should be partly removed.

There is a great need to improve the landscape quality around stormwater ponds. For this reason, the construction of stormwater ponds should be designed in connection with other water bodies to act as stepping stones. Consequently, we recommend enhancing the connectivity between stormwater ponds through the creation of urban green spaces and new ponds along potential dispersal corridors. Taxa other than dragonflies would also benefit from a greater extent of ponds that are connected by semi-natural habitats (Snep et al., 2006; Gledhill et al., 2008; Holtmann et al., 2017).

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Appendix A. Statistics of single GLM (at the habitat level), habitat models, and landscape models: Relationship between species number (a), adult density (b) and exuviae density (c) and all environmental parameters at stormwater ponds (STO) and control ponds (CON). − signifies negative relationship, + signifies positive relationship, Thre = threatened, Medi = Mediterranean, Eur = Eurasian, spec = species, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. = not significant.

a) Species richness

Parameter	STO	CON	STO	CON	STO	CON
	Thre spec		Medi spec		Eur spec	
Single GLM						
Structural parameters						
Size	n.s.	n.s.	n.s.	+**	n.s.	+**
Depth	n.s.	n.s.	n.s.	n.s.	+*	n.s.
Hydrological parameters						
pH value	n.s.	n.s.	+*	n.s.	n.s.	n.s.
Conductivity	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Water temperature	+*	n.s.	n.s.	n.s.	n.s.	n.s.
Chloride	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Nitrate	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Phosphate	n.s.	n.s.	n.s.	−*	n.s.	n.s.
Ammonium	n.s.	n.s.	n.s.	−**	n.s.	n.s.
Potassium	n.s.	−*	−**	n.s.	−*	n.s.
Vegetation cover						
Open water surface	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Reed bed	n.s.	n.s.	−*	n.s.	n.s.	n.s.
Algae	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Floating leaf plants	n.s.	n.s.	n.s.	−*	n.s.	n.s.
Submerged aquatic plants	n.s.	+**	n.s.	n.s.	n.s.	n.s.
Riparian woodland	n.s.	−*	n.s.	−***	n.s.	−*
Categorical variables						
Fish (baseline: present) absent	n.s.	−*	−*	−***	n.s.	−**
Hydroperiod (baseline: permanent) temporary	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Habitat model						
Size	.	.	.	.	.	+*
Depth	.	.	.	.	+*	.
Water temperature	+*	.	.	.	.	.
Phosphate	.	.	.	−*	.	.
Ammonium	.	.	.	−**	.	.
Riparian woodland	.	−*	.	−***	.	.

R^2 (McFadden)	0.13	0.35	n.s.	0.52	0.12	0.24
Landscape model						
Built-up area	.	.	−***	.	−**	−*
R^2 (McFadden)	n.s.	n.s.	0.39	n.s.	0.36	0.07

b) Adult density

Parameter	STO	CON	STO	CON	STO	CON
	Thre spec		Medi spec		Eur spec	
Single GLM						
Structural parameters						
Size	+*	n.s.	n.s.	+***	n.s.	n.s.
Depth	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Hydrological parameters						
pH value	n.s.	n.s.	+**	n.s.	+**	n.s.
Conductivity	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Water temperature	+**	n.s.	+**	n.s.	n.s.	n.s.
Chloride	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Nitrate	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Phosphate	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Ammonium	n.s.	n.s.	n.s.	n.s.	n.s.	−*
Potassium	−*	n.s.	−**	n.s.	−*	n.s.
Vegetation cover						
Open water surface	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Reed bed	n.s.	n.s.	−*	n.s.	n.s.	n.s.
Algae	+*	n.s.	n.s.	n.s.	n.s.	n.s.
Floating leaf plants	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Submerged aquatic plants	n.s.	+**	n.s.	n.s.	n.s.	n.s.
Riparian woodland	n.s.	n.s.	n.s.	−**	n.s.	n.s.
Categorical variables						
Fish (baseline: present) absent	n.s.	n.s.	n.s.	n.s.	−*	−*
Hydroperiod (baseline: permanent) temporary	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Habitat model						
Size	+***	.	.	.	.	.
Ammonium	.	.	.	.	.	−***
Algae	+*	.	.	.	.	.
Submerged vegetation	.	+*	.	.	.	.
Riparian woodland	.	.	.	−**	.	.
R^2 (McFadden)	0.42	0.42	n.s.	0.19	n.s.	0.30
Landscape model						
Grassland	−**	.	.	.	.	.
Woodland	.	.	.	.	+**	.
Built-up area	−***	.	−**	−**	−**	.
Distance to next three ponds	−***	.	.	.	−***	.
R^2 (McFadden)	0.38	n.s.	0.22	0.16	0.39	n.s.

c) Exuviae density

Parameter	STO	CON	STO	CON	STO	CON
	Thre spec		Medi spec		Eur spec	
Single GLM						
Structural parameters						
Size	+***	+*	n.s.	n.s.	n.s.	+***
Depth	+***	n.s.	+*	n.s.	−**	+*
Hydrological parameters						
pH value	n.s.	n.s.	+***	n.s.	n.s.	−**

Conductivity	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Water temperature	+*	n.s.	+*	n.s.	n.s.	n.s.
Chloride	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Nitrate	n.s.	n.s.	−**	n.s.	−**	n.s.
Phosphate	n.s.	n.s.	n.s.	−**	n.s.	−**
Ammonium	−*	n.s.	n.s.	n.s.	n.s.	n.s.
Potassium	n.s.	−*	−***	n.s.	n.s.	n.s.
Vegetation cover						
Open water surface	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Reed bed	n.s.	n.s.	−**	n.s.	−**	n.s.
Algae	n.s.	n.s.	n.s.	n.s.	n.s.	+*
Floating leaf plants	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Submerged aquatic plants	n.s.	+*	+*	n.s.	n.s.	+*
Riparian woodland	−*	−*	n.s.	n.s.	n.s.	n.s.
Categorical variables						
Fish (baseline: present) absent	n.s.	−**	n.s.	n.s.	n.s.	−**
Hydroperiod (baseline: permanent) temporary	n.s.	n.s.	−*	n.s.	n.s.	n.s.
Habitat model						
Size	+***	.	.	.	.	+*
Depth	+***	.	+***	.	.	.
Phosphate	.	.	.	−**	.	−*
Reed bed	.	.	.	.	−*	.
Riparian woodland	−**	−**	.	.	.	.
Submerged vegetation	.	.	+***	.	.	+*
R^2 (McFadden)	0.47	0.27	0.34	0.23	0.13	0.39
Landscape model						
Woodland	.	.	+***	.	.	.
Built-up area	.	.	.	−*	−***	−**
Distance to next three ponds	−***	.	.	.	.	.
R^2 (McFadden)	0.14	n.s.	0.46	0.19	0.27	0.28

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