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Habitat heterogeneity determines plant species richness in urban stormwater ponds

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ABSTRACT

Urbanisation is seen as one of the most important drivers for species extinction. The aim of our study was to compare vascular plant species richness of 35 artificial urban stormwater ponds (STOPON) designed to control water flow, with 35 control ponds (CONTROL) in the surrounding landscape. For both plot types, we gathered a variety of environmental parameters to determine the drivers of plant species richness. Based on the results, we discuss the relevance of STOPON for biodiversity conservation in urban areas and give recommendations for biodiversity-friendly construction and pond management.

Our study showed that the environmental conditions clearly varied between STOPON and CONTROL. STOPON were especially larger than CONTROL; as a consequence, the aquatic, semi-aquatic and terrestrial zones had a greater extent at STOPON. Accordingly, the overall and mean number of aquatic, salt-tolerating aquatic and threatened plant species was higher at STOPON than at CONTROL. However, species density of all three plant indicator groups did not differ among the two plot types.

The greater plant species richness of STOPON was driven by a higher habitat heterogeneity which was especially explained by (i) the genuine effect of habitat area on habitat heterogeneity, (ii) the existence of three similarly large habitat zones (terrestrial, semi-aquatic, aquatic) and (iii) the regular management, which represses shading plants, creates open soil and activates the soil seed bank. Due to the high species richness of threatened plant species STOPON play an important role in biodiversity conservation in urban areas.

1. Introduction

The loss of global biodiversity is one of the major challenges of our time. Global extinction rates of plant and animal species have risen continually over recent decades and are currently 1000 times higher than expected (De Vos et al., 2014). Despite great efforts in nature conservation, this dramatic trend is still ongoing (Butchart et al. 2010). Hence, Barnosky et al. (2011) suspect that we are on the way to Earth's sixth mass extinction. For terrestrial biomes, land-use change is presumed to be the main cause of this biodiversity crisis (Sala et al., 2000).

Worldwide urban areas are the most rapidly growing land-use type (United Nations, 2010). Among land-use change, urbanisation is seen as one of the most important drivers for species extinction (McKinney, 2006; Grimm et al., 2008). Directly, urbanisation leads to a loss of natural and semi-natural habitats by impervious surfaces (Balmford et al., 2003; McKinney, 2006; Steele and Heffernan, 2014). Consequently, reduced size of the remaining habitats and an increasing fragmentation are indirect effects (Lambin et al., 2001; Fahrig, 2003; Donnelly and Marzluff, 2006). Moreover, habitat quality is often reduced (Grimm et al., 2008).

These negative effects of urbanisation are particularly true for water bodies in urban areas as they are customised 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). Consequently, greater cover of impervious surfaces disturbs the hydrologic balance resulting in a higher run-off magnitude and an increasing flood frequency (Ehrenfeld, 2000; Steele and Heffernan, 2014). To mitigate the negative hydrologic effects of urbanisation, there has been an increase in the construction of stormwater ponds during recent decades (Herrmann, 2012). Stormwater ponds are designed to moderate run-off from impervious surfaces because they are able to temporarily withhold large quantities of water (Villareal et al., 2004; Gallagher et al., 2011).

According to Hobbs et al. (2006), stormwater ponds are novel ecosystems. Novel ecosystems are characterised by (i) novelty, i.e. new species combinations and (ii) human action, which means that they are always the result of intentional or unintentional human activities

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(Hobbs et al., 2006; Hermann et al., 2013). A growing number of studies indicate that stormwater ponds do not only fulfil a retention function, but they also serve as a habitat for aquatic and semi-aquatic species (USA: Birx-Raybuck et al., 2010; Brand and Snodgrass, 2010; Canada: Hassall and Anderson, 2015; France: Scher and Thièry, 2005; Le Viol et al., 2009, 2012; Australia: Hamer et al., 2012). In contrast to the mentioned studies from North America and Australia, there are virtually no studies on the conservation value of urban stormwater ponds in Central Europe; apart from the recent studies by Holtmann et al. (2017, 2018, 2019).

All aforementioned papers on the biodiversity of stormwater ponds concentrated on animal species (amphibians, odonates and macroinvertebrates). In contrast, there is no systematic study investigating vascular plants on a larger sample of stormwater ponds. Herrmann (2012) analysed the vegetation of a single stormwater wetland in Sweden during the first four years after construction. Solga (2001) demonstrated the high importance of stormwater ponds in Germany for rare and endangered moss species. In general, small water bodies are known to be important habitats for aquatic and semi-aquatic vascular plants. In comparison to other types of water bodies, they usually have a higher phytodiversity. This is particularly true for rare and endangered species (Nicolet et al., 2004; Davies et al., 2008).

The aim of our study was to compare vascular plant species richness of 35 artificial urban stormwater ponds, designed to control water flow, with 35 control ponds in the surrounding landscape. For both plot types we gathered a variety of environmental parameters to determine the drivers of plant species richness. Based on the results, we discuss the relevance of stormwater ponds for biodiversity conservation in urban areas and give recommendations for biodiversity-friendly construction and management of the ponds.

2. Material and methods

2.1. Study area

The study area is located in the northern part of the German Federal State of North Rhine-Westphalia and comprises the municipal area of the city of Münster (51°58″N, 7°38″E; 39–99 m a.s.l.) (Fig. 1). On an area of 303 km^2, the city of Münster has 308,000 inhabitants (City of Münster, 2017). Of the total area, 34% consists of built-up and traffic areas; agricultural land covers 46%, forests 18% and water bodies 2%. Biogeographically, the study area is a part of the Westphalian Basin which belongs to in the North German Plain. The climate is suboceanic with annual precipitation of 780 mm and a mean annual temperature of 9.9 °C (1981–2010; climate station Münster/Osnabrück; DWD, 2018).

Currently, 79 stormwater ponds exist in the study area (Möhring pers. comm., Civil Engineering Office Münster). Soil application, as well as planting and sowing of plants, has never occurred at any of the stormwater ponds within the study area. Their banks are usually not paved or concreted and all ponds are regularly managed to ensure a maximum water retention volume. Management includes cutting of woody riparian plants and desludging of ponds every couple of years. The herb layer is usually cut every year in winter.

2.2. Sampling design

2.2.1. Plots

The study was conducted during the growing season in 2016. In total, we studied 70 plots, 35 randomly selected stormwater ponds (STOPON) and 35 control ponds (CONTROL). A control pond was defined as the next pond in the vicinity of each chosen STOPON (mean distance 781 m ± 99 m SE) (cf. Holtmann et al., 2017, 2018).

2.2.2. Plant indicator groups

Plant species surveys comprised the three following indicator groups:

(i) Semi-aquatic and aquatic species (hereafter referred to as aquatic plants): plants with an Ellenberg moisture indicator value (F) of ≥ 8 (i.e.; indicator of wetness or aquatic plants), indicators of strong water level fluctuations (~) or indicators of flooding (=) (Ellenberg and Leuschner, 2010) (cf. Brose, 2001).
(ii) Semi-aquatic and aquatic species (F ≥ 8) with an Ellenberg salt indicator value (S) of ≥ 1 (salt-tolerant plants) (hereafter referred to as salt-tolerating aquatic plants) (Ellenberg and Leuschner, 2010).
(iii) Threatened species according to the red data book of North Rhine-Westphalia (LANUV NRW, 2010).

Plant species were sampled twice in June and July with at least three weeks between each visit. Per visit, all habitat structures of a plot were surveyed in loops for the occurrence of plant species within the three indicator groups during a standardised time of two hours. Additionally, to detect aquatic plants in deeper parts of the water bodies, we used a stick (length: 1.2 m) with hooks at the end. Plant species were identified according to Oberdorfer (2001), van de Weyer et al. (2011) and Jäger et al. (2013). The scientific nomenclature follows Wisskirchen and Haeupler (1998).

2.2.3. Environmental parameters

For each plot, we sampled several environmental parameters (Tables 1 and 2). Per plot, we calculated the size using aerial photographs (Bezirksregierung Köln, 2018) and ArcGIS 10.2. The soil type was determined after Geologischer Dienst NRW (GD NRW, 2018) (Table 2). Conductivity, pH and water level were measured during both visits (Table 1). Prior to statistical analysis, the data were averaged per parameter and plot. All other environmental parameters were recorded during the visit in July.

Although, for the majority of the stormwater ponds data concerning their age were available (Möhring pers. comm., Civil Engineering Office Münster), pond age was a poor predictor of environmental conditions at the ponds. All stormwater ponds are regularly managed (cf. Section 2.1), but the intervals depend on the successional speed of each pond. Hence, even old ponds can represent early successional stages when they have recently been managed including desludging. Data on the management measures, however, were not available (Möhring pers. comm., Civil Engineering Office Münster). As a result, we measured the cover of different vegetation layers in the aquatic zone (water body) as well as the height of the terrestrial and semi-aquatic herb layer to reflect the successional stage of the plots (Table 1).

Additionally, aboveground biomass was sampled to evaluate nutrient conditions (Table 1). Samples were taken at three random sites of 40 cm × 40 cm in the terrestrial/semi-aquatic zone of the plot, where vegetation was cut 2 cm above ground. Samples were mixed, dried at 105 °C, ground with a mill, and sifted through a sieve with a mesh wire of 0.5 mm (Kleinebecker et al., 2009). The milled samples were subsequently analysed by near-infrared reflectance spectroscopy (NIRS [Spectra Star 2400, Unity Scientific, Columbia, MD, USA]) for the nutrition elements phosphate (P), potassium (K) and nitrogen (N).

Cover data of (i) the three habitat zones (terrestrial, semi-aquatic and aquatic) of a plot and (ii) the different vegetation layers in the aquatic zone (i.e., open water surface, submerged aquatic plants, algae, floating aquatic plants and reed bed; Table 1) were used to compute two Shannon indices (Pielou, 1975) as indicators of plot heterogeneity and water body heterogeneity, respectively (Table 1):

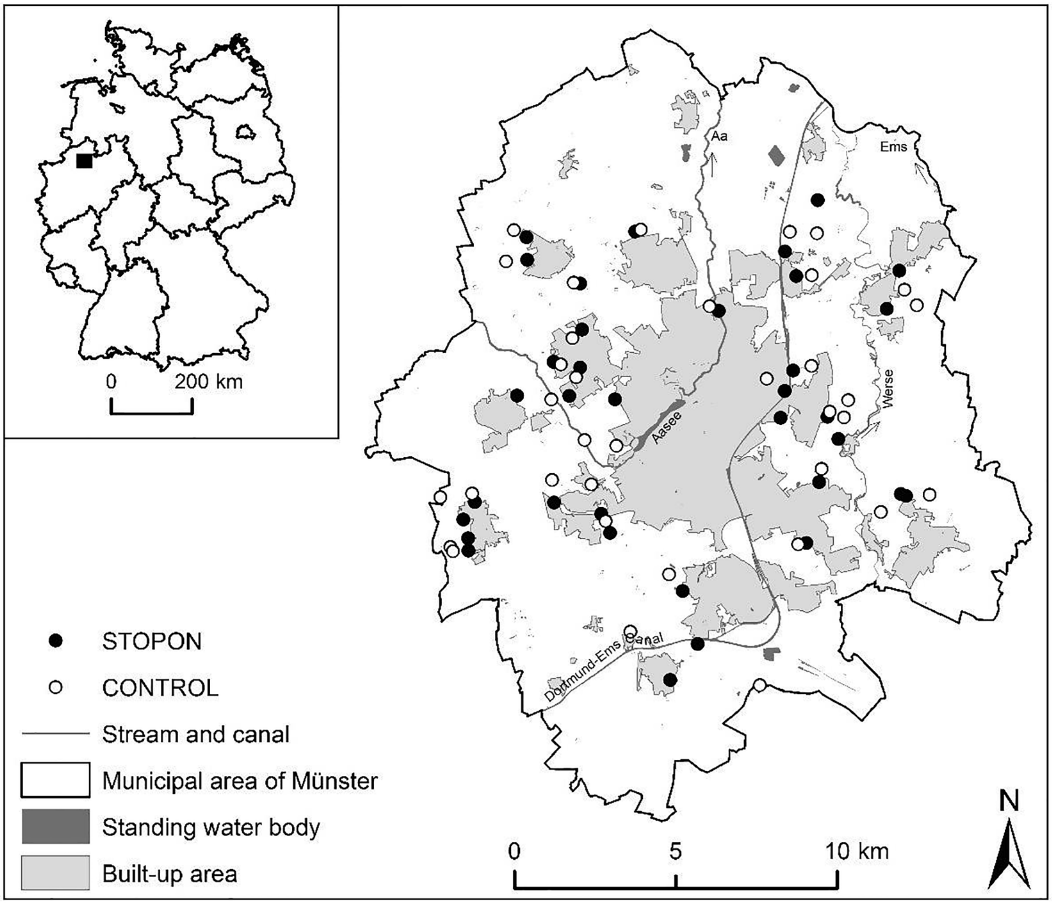

Fig. 1. Location of surveyed stormwater ponds (STOPON) and control ponds (CONTROL) in the municipal area of Münster (NW Germany).

$$H' = -\sum_i p_i \times \ln p_i \text{ with } p_i = \frac{n_i}{N}$$

where p_i is the relative proportion of all habitat zones and vegetation layers, formed by type i, respectively. n_i represents the area covered by each habitat zone and vegetation layer, respectively.

2.3. Statistical analysis

All numerical data were visually checked in histograms for normal distribution and homogeneity of variance (Quinn and Keough, 2002). 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 data were normally distributed; otherwise, a Wilcoxon Signed Rank test was conducted (Table 1). Differences in absolute frequencies between the soil types of both plot types were analysed with the Fisher's exact test (Table 2).

We determined a significant linear relationship (linear regression) between the number of plant species of the three indicator groups with plot size (threatened species [STOPON: $P < 0.001$, $R^2 = 0.44$; CONTROL: $P < 0.05$, $R^2 = 0.13$]) and the size of the semi-aquatic/aquatic zone (aquatic [STOPON: $P < 0.001$, $R^2 = 0.29$; CONTROL: $P < 0.01$, $R^2 = 0.28$] and salt-tolerating aquatic species [STOPON: $P < 0.01$, $R^2 = 0.27$; CONTROL: $P < 0.01$, $R^2 = 0.17$]), respectively. As a consequence, we calculated the species density (no. species/ $100\,m^2$) with plot size and size of the semi-aquatic/aquatic zone, respectively, as the basis.

Prior to multivariate analyses, Spearman rank correlations (r_s) of all numerical variables listed in Table 1 were conducted to identify those with strong inter-correlations ($|r_s| \geq 0.5$) (Dormann et al., 2013). As a result, the variables plot size, terrestrial area, height semi-aquatic herb layer, sunshine duration, nitrogen, potassium, open water surface, submerged aquatic plants and reed bed were excluded from the following analyses (Appendix A).

We tested all three plant indicator groups for spatial autocorrelation by calculating Global Moran's I (Diniz-Filho et al., 2003; Legendre and Legendre, 2012) with ArcGIS 10.2 prior to analyses. Since there were no significant results ($P > 0.05$), spatial autocorrelation was rejected.

In order to determine the relationship between species number of each of the three plant indicator groups and environmental parameters at STOPON and CONTROL, we computed generalised linear models (GLM) (Crawley, 2007). At first, we conducted a GLM for each environmental parameter separately (Appendix B) to reduce the number of predictor variables and to avoid an over-fitting (Dormann et al., 2013; Löffler and Fartmann, 2017). Only significant variables were integrated into a synthesis model (Table 4). In order to increase model robustness and identify the most important environmental parameters in the synthesis models, we conducted model averaging based on an information-theoretic approach (Burnham and Anderson, 2002; Grueber et al., 2011). Model averaging was conducted using the 'dredge' function (R package MuMIn, Bartón, 2016) and only included top-ranked models within $\Delta AIC_C < 3$ (cf. Grueber et al., 2011).

Table 1
Overview of sampled predictor parameters (mean ± 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 Signed Rank test (*W*). Significant differences between the two plot 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.	
Plot size (m²)[a]	3,386 ± 455	390–9,048	652 ± 129	18–3,387	***W******
Area habitat zone (m²)					
Terrestrial	1,150 ± 216	45–5,794	186 ± 45	5–1,281	***W******
Semi-aquatic	1,339 ± 309	0–6,976	101 ± 23	0–664	***W******
Aquatic	897 ± 183	13–5,033	366 ± 96	10–2,710	***W****
Terrestrial and semi-aquatic zone					
Nutrient content biomass (%)[b]					
Nitrogen	1.4 ± 0.0	1.0–2.3	2.3 ± 0.1	1.1–4.0	***t******
Phosphate	0.2 ± 0.0	0.2–0.3	0.3 ± 0.0	0.2–0.4	***t******
Potassium	1.3 ± 0.1	0.6–3.0	1.6 ± 0.1	0.0–2.9	***t****
Vegetation height (cm)					
Terrestrial herb layer	67.3 ± 5.5	30–200	49.7 ± 6.0	5–120	***t****
Semi-aquatic herb layer	74.3 ± 7.9	0–190	38.9 ± 7.7	0–150	***t*****
Aquatic zone (water body)					
Depth (cm)	34.9 ± 3.3	5–86	53.7 ± 5.4	5–136	***t*****
Hydrology					
Conductivity (µS/cm)[c]	626.1 ± 51.4	94–1,443	495.4 ± 58.5	123–1,913	***W****
pH[c]	7.8 ± 0.2	6.5–9.9	7.5 ± 0.1	6.1–9.5	*t*$^{n.s.}$
Water level fluctuation (cm)	6.4 ± 0.8	0–21	13.9 ± 1.7	0–35	***t******
Sunshine duration (h/d)[d]	10.6 ± 0.7	1.8–16.0	5.7 ± 0.8	0.0–16.0	***t******
Vegetation cover (%)					
Open water surface	46.7 ± 6.4	0–100	62.6 ± 6.6	0–100	*t*$^{n.s.}$
Submerged aquatic plants	5.7 ± 3.2	0–95	3.1 ± 1.8	0–55	*W*$^{n.s.}$
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*$^{n.s.}$
Reed bed	36.8 ± 6.2	0–100	13.0 ± 3.6	0–75	***t*****
Riparian woodland	19.9 ± 4.1	0–80	49.6 ± 5.5	0–100	***t******
Open soil	8.1 ± 2.0	0–60	11.3 ± 2.9	0–70	*W*$^{n.s.}$
Habitat heterogeneity (Shannon index)					
Plot heterogeneity[e]	0.8 ± 0.0	0.2–1.1	0.7 ± 0.0	0.0–1.1	*t*$^{n.s.}$
Water body heterogeneity[f]	0.5 ± 0.1	0.0–1.3	0.4 ± 0.1	0.0–1.1	*t*$^{n.s.}$

[a] Calculated from aerial photographs by using ArcGIS 10.2.
[b] Content in above ground biomass determined using near-infrared reflectance spectroscopy (NIRS [Spectra Star 2400, Unity Scientific]).
[c] Measured by using a multi-parameter probe (Hanna HI 98129).
[d] Measured in June in hours of potential sunshine per day by using a horizontoscope after Tonne (1954); mean of four measures at N, E, S, W.
[e] Calculated using the area of the terrestrial, semi-aquatic and aquatic zone of the plot.
[f] Calculated using the cover of all vegetation layers of the aquatic zone (water body).

Table 2
Absolute and relative frequencies of the categorical variable soil type at stormwater ponds (STOPON) and control ponds (CONTROL). Differences in absolute frequencies between the two plot types were analysed with Fisher's exact test. n.s. not significant.

Parameter	STOPON		CONTROL		P
	N	%	N	%	
Soil type					n.s.
Sand	6	17.1	5	14.3	
Silty sand	13	37.1	11	31.4	
Silty clay	16	45.7	19	54.3	

All analyses were performed using R-3.4.3 (R Development Core Team, 2018), SigmaPlot 13.0 and IBM SPSS Statistics 23.

3. Results

3.1. Environmental parameters

Most of the environmental parameters differed between STOPON and CONTROL (Table 1). STOPON were larger than CONTROL; as a consequence, the aquatic, semi-aquatic and terrestrial zones had a greater expansion at STOPON (all three variables were positively correlated with plot size; Appendix A). Additionally, STOPON were more nutrient-poor (contained lower levels of nitrogen, phosphate and potassium) and had a taller herb layer than CONTROL. The water bodies at STOPON were shallower, had a higher conductivity and cover of reed bed, their water level fluctuated less and due to a lower cover of riparian woodland, they were more sunlit than those at CONTROL (Table 1). The remaining numerical parameters (Table 1) and the soil type (Table 2) did not differ between the two plot types.

3.2. Plant indicator groups

3.2.1. Species richness and density

At the 70 plots we recorded a total of 91 aquatic, 30 salt-tolerating aquatic and 37 threatened plant species (Table 3). For all three indicator groups, the number of observed species was higher at STOPON than at CONTROL. At STOPON we detected 86 aquatic, 29 salt-tolerating and 34 threatened plant species; the respective figures for CONTROL were 56, 19 and 12.

At STOPON, the most frequent aquatic plant species were *Juncus inflexus* and *Typha latifolia*, both of which occurred at 74% of the plots

Table 3
Frequencies (%) of all detected plant species at stormwater (STOPON) and control ponds (CONTROL). Aqua = Aquatic plants, Salt = salt-tolerating aquatic plants, Threat = threatened plants. For further information cf. Section 2.2.2.

Species	STOPON	CONTROL	Aqua	Salt	Threat
Agrostis stolonifera	40	3	x	.	.
Alisma lanceolatum	9	3	x	.	.
Alisma plantago-aquatica	69	14	x	.	.
Alopecurus aequalis	9	0	x	.	x
Alopecurus geniculatus	14	3	x	x	.
Berula erecta	11	0	x	x	.
Butomus umbellatus	14	0	x	.	x
Callitriche spec.	54	9	x	.	.
Caltha palustris	9	3	x	.	x
Carex acuta	14	17	x	.	.
Carex acutiformis	3	0	x	.	.
Carex demissa	14	0	x	.	x
Carex distans	3	0	x	x	x
Carex disticha	14	9	x	.	.
Carex elata	6	0	x	.	x
Carex flacca	26	14	x	x	.
Carex flava	6	0	x	.	x
Carex hirta	57	17	x	.	.
Carex leporina	11	0	x	.	.
Carex muricata	17	0	.	.	x
Carex nigra	17	0	x	x	x
Carex otrubae	60	14	x	x	.
Carex pallescens	6	0	x	.	.
Carex panicea	3	0	x	x	x
Carex paniculata	6	0	x	.	x
Carex pendula	17	3	x	.	.
Carex pseudocyperus	60	20	x	.	.
Carex remota	37	37	x	.	.
Carex riparia	6	0	x	.	x
Carex vesicaria	0	3	x	.	x
Carex viridula	14	0	x	x	x
Centaurium erythraea	14	0	.	.	x
Centaurium pulchellum	23	0	x	x	x
Ceratophyllum demersum	9	6	x	.	.
Dactylorhiza maculata agg.	6	0	x	.	x
Dactylorhiza majalis	6	0	x	.	x
Eleocharis acicularis	3	0	x	.	x
Eleocharis multicaulis	9	3	x	x	x
Eleocharis palustris	66	14	x	.	x
Eleocharis quinqueflora	3	0	x	x	x
Epilobium hirsutum	37	6	x	x	.
Epilobium palustre	9	0	x	.	x
Equisetum fluviatile	6	3	x	.	.
Equisetum palustre	26	9	x	.	.
Galium palustre	31	6	x	.	.
Glyceria fluitans	14	9	x	.	.
Hypericum tetrapterum	6	0	x	.	.
Iris pseudacorus	40	40	x	.	.
Isolepis setacea	29	0	x	.	x
Juncus articulatus	66	17	x	x	.
Juncus bufonius	11	6	x	.	.
Juncus compressus	23	6	x	x	.
Juncus conglomeratus	37	6	x	.	.
Juncus inflexus	74	20	x	x	.
Lemna minor	60	40	x	x	.
Lemna trisulca	6	9	x	x	x
Lychnis flos-cuculi	3	3	x	.	x
Lysimachia nummularia	29	6	x	.	.
Lysimachia thyrsiflora	3	0	x	.	x
Lysimachia vulgaris	34	6	x	.	.
Lythrum salicaria	51	14	x	x	.
Mentha aquatica	69	17	x	.	.
Myosotis laxa	29	0	x	.	x
Myosotis scorpioides	46	3	x	.	.
Myriophyllum spicatum	0	3	x	.	.
Nasturtium officinale	57	0	x	.	.
Nuphar lutea	3	6	x	.	.
Ophioglossum vulgatum	3	0	.	x	x
Persicaria amphibia	6	0	x	.	.
Phalaris arundinacea	49	3	x	.	.
Phragmites australis	46	6	x	.	.
Potamogeton berchtoldii	9	6	x	x	.
Potamogeton crispus	9	0	x	x	.
Potamogeton gramineus	0	3	x	.	x
Potamogeton natans	3	11	x	.	.
Potamogeton pusillus	23	3	x	x	.
Pulicaria dysenterica	6	0	x	.	.
Ranunculus aquatilis	6	3	x	.	x
Ranunculus flammula	0	3	x	x	x
Ranunculus peltatus	0	9	x	.	.
Ranunculus sceleratus	26	3	x	x	.
Samolus valerandi	17	0	x	x	x
Schoenoplectus lacustris	3	0	x	x	x
Schoenoplectus tabernaemontani	43	9	x	x	x
Scirpus sylvaticus	20	3	x	.	.
Scutellaria galericulata	3	0	x	.	.
Sparganium erectum	3	0	x	.	.
Spirodela polyrhiza	6	6	x	x	x
Typha angustifolia	37	6	x	x	.
Typha latifolia	74	11	x	x	.
Utricularia australis	3	6	x	.	x
Veronica anagallis-aquatica	20	0	x	.	.
Veronica beccabunga	57	0	x	.	.
Veronica catenata	9	3	x	.	.

(26 plots), followed by *Alisma plantago-aquatica* and *Mentha aquatica*, each found at 69% of the plots (24 plots). At CONTROL, *Iris pseudacorus* and *Lemna minor* were the most widespread species having constancy of 40% (14 plots each), followed by *Carex remota* (37%, 13 plots). Three of these species, *J. inflexus*, *L. minor* and *T. latifolia*, also belonged to the group of salt-tolerating aquatic species. The most widespread threatened species at STOPON were *Eleocharis palustris* (constancy of 66%), *Schoenoplectus tabernaemontani* (43%), *Isolepis setacea* (29%), *Myosotis laxa* (29%) and *Centaurium pulchellum* (23%). At CONTROL, *Eleocharis palustris* was the most frequent threatened species with constancy of 14%. Species richness of aquatic, salt-tolerating aquatic and threatened plant species was significantly higher at STOPON than at CONTROL (Fig. 2a). Species density of all three indicator groups, however, did not differ among the two plot types (Fig. 2b).

3.2.2. *Response of indicator groups to environmental conditions*

The response of the three plant indicator groups to environmental conditions was similar among the groups and the two plot types (Table 4). The most important environmental parameter was water body heterogeneity which had a positive effect on species richness of all three indicator groups at STOPON and CONTROL. The relationship between the cover of riparian woodland and species richness of aquatic and salt-tolerating aquatic plants was negative at both plot types. Additionally, at STOPON the area of the semi-aquatic zone also had positive effects on species richness of salt-tolerating aquatic and threatened plants. Generally, the explanatory power of the models was high (McFadden Pseudo-R^2: 0.22–0.45).

4. Discussion

Our study showed that the environmental conditions clearly varied between STOPON and CONTROL, confirming previous findings from the same study area (Holtmann et al., 2017, 2018). STOPON were especially larger than CONTROL; as a consequence, the aquatic, semi-aquatic and terrestrial zones had a greater extent at STOPON. Accordingly, the overall and the mean number of aquatic, salt-tolerating aquatic and threatened plant species were higher at STOPON than at CONTROL. Species density of all three plant indicator groups, however, did not differ among the two plot types.

It is a biogeographical theory that species richness increases with rising habitat area (Arrhenius, 1921; MacArthur and Wilson, 1963, 1967; Rosenzweig, 1995). This relationship has been acknowledged by

Table 4

Model averaging results (GLM, synthesis models): Relationship between species number of aquatic plants (a), salt-tolerating aquatic plants (b), threatened plants (c) and environmental parameters at stormwater ponds (STOPON) and control ponds (CONTROL), respectively. Model-averaged coefficients (conditional average) were derived from the top-ranked models ($\Delta AIC_C < 3$). All global 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. $R2_{MF}$ = Range of McFadden's Pseudo R^2 of the top-ranked models ($\Delta AIC_C < 3$).

STOPON				CONTROL			
Parameter	Estimate	SE	*P*	Parameter	Estimate	SE	*P*
a) Aquatic species							
$R^2_{MF} = 0.29–0.41$				$R^2_{MF} = 0.32–0.45$			
Intercept	2.591	0.179	***	Intercept	1.913	0.383	***
Riparian woodland	–0.007	0.003	*	Riparian woodland	–0.016	0.005	***
Water body heterogeneity	0.806	0.270	**	Water body heterogeneity	0.878	0.358	*
b) Salt-tolerating aquatic species							
$R^2_{MF} = 0.37–0.42$				$R^2_{MF} = 0.43$			
Intercept	1.731	0.141	***	Intercept	0.703	0.287	*
Riparian woodland	–0.008	0.003	**	Riparian woodland	–0.017	0.004	***
Water body heterogeneity	0.613	0.224	**	Water body heterogeneity	1.369	0.367	***
Semi-aquatic area	0.000	0.000	*				
c) Threatened species							
$R^2_{MF} = 0.22–0.31$				$R^2_{MF} = 0.26–0.38$			
Intercept	0.510	0.334	n.s.	Intercept	–0.962	0.561	n.s.
Semi-aquatic area	0.000	0.000	*	Water body heterogeneity	1.840	0.637	**
Water body heterogeneity	1.284	0.526	*				

several studies (e.g. Gee et al., 1997; Oertli et al., 2002; Krauss et al., 2004; Field et al., 2009; Beninde et al., 2015). According to the habitat heterogeneity hypothesis, habitat area is a surrogate of habitat heterogeneity (Brose, 2001; Steinmann et al., 2011). Habitat heterogeneity is associated with a higher availability of microsites; as a result, larger habitats exhibit a wider range of microhabitats and, hence, higher species richness (Williams, 1964; Connor and McCoy, 1979; Williamson, 1981; Brose, 2001). In line with this, the differences in species richness of aquatic, salt-tolerating aquatic and threatened plant species between STOPON and CONTROL in our study were attributed to the unequal habitat size as species density did not differ.

Habitat heterogeneity was also the main driver of plant species richness in the GLM. In all six models, species richness was positively related to water body heterogeneity and in two models (salt-tolerating aquatic and threatened plant species at STOPON) to the area of the semi-aquatic zone – a substitute for habitat heterogeneity (cf. above). At CONTROL the clearly dominating habitat zone was the aquatic one (Table 1). Hence, species richness of aquatic, salt-tolerating aquatic and threatened plant species should especially depend on the area of this zone; which was indeed the case. In contrast, at STOPON, the semi-aquatic zone was larger on average than the aquatic zone (Table 1). Hence, it should be relevant for plant species richness, too. In fact, species richness of salt-tolerating aquatic and threatened plant species increased also with the size of the semi-aquatic zone.

The third predictor of plant species richness was the cover of riparian woodland. It was negatively correlated with the daily sunshine duration in June (Appendix A) and had a negative effect on species richness of aquatic and salt-tolerating aquatic plants at both STOPON and CONTROL. Generally, light availability is a key factor for plants in temperate zones as water and nutrients are usually not limiting (Ellenberg and Leuschner, 2010). Light availability determines assemblage composition, i.e. species recruitment, growth, reproduction, and species richness (Kotowski and van Diggelen, 2004; Lacoul and Freedman, 2006). Light attenuation varies among plant communities and is related to productivity and canopy structure (Fliervoet, 1984; Russell et al., 1989; Kotowski and van Diggelen, 2004). In general, species richness decreases with shading (Kotowski and van Diggelen, 2004; Schrautzer and Jensen, 2005; Hassall et al., 2011; Thornhill et al.,

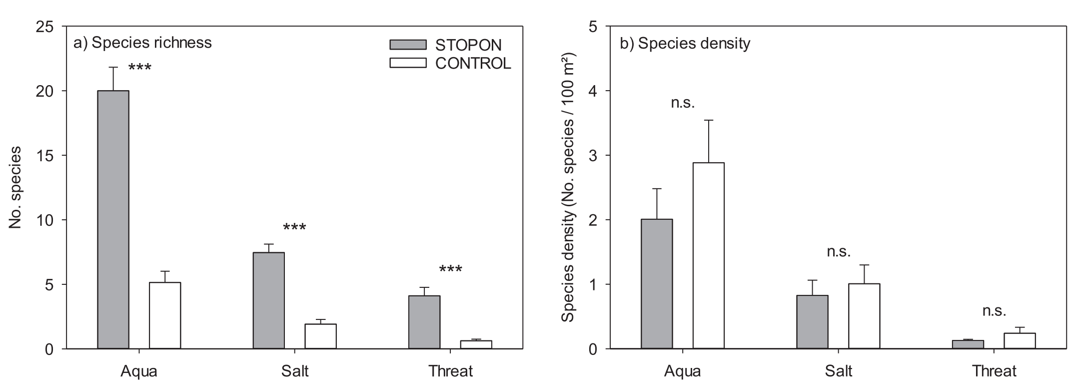

Fig. 2. Mean (± SE) species richness (a) and species density (b) of aquatic (Aqua), salt-tolerating aquatic (Salt) and threatened plant species (Threat) at stormwater ponds (STOPON) and control ponds (CONTROL). Differences between the two plot types were tested using paired *t* test (species richness of aquatic and salt-tolerating aquatic species) or Wilcoxon Signed Rank test (all other response variables), respectively. Species richness (a) – Aqua: $t = 7.55$, $df = 34$, $P < 0.001$; Salt: $t = 7.19$, $df = 34$, $P < 0.001$; Threat: $P < 0.001$. Species density (b) – Aqua: $P = 0.25$; Salt: $P = 0.86$; Threat: $P = 0.54$. *** $P < 0.001$, n.s. not significant.

2017).

Compared to the plots in the surrounding landscape, STOPON were considerably larger and usually consisted of three similarly big habitat zones (cf. Table 1) due to very shallow slopes (own observation). In contrast, CONTROL were much smaller and due to steep slopes (own observation) usually dominated by only one habitat zone, the aquatic zone. Besides the large size of STOPON with its usually beneficial effects on habitat heterogeneity and species richness (see above), the existence of three similarly large habitat zones also contributed to the enhanced species richness (cf. Keddy, 1991; Pollock et al., 1998; Brose, 2001). Moreover, due to regular management (cf. Section 2.1), the habitat quality at STOPON was generally high (cf. Holtmann et al., 2017, 2018). STOPON were more nutrient-poor (lower nitrogen, phosphate and potassium content) and sunlit than CONTROL. Desludging of STOPON and cutting of woody riparian plants every couple of years, as well as yearly cutting of the herb layer, removes accumulated nutrients, slows down succession and results in sunny microhabitats. Hence, the presence of conditions that generally favour a high plant species richness (see above). Additionally, the mowing vehicles regularly activate existing seed banks by causing microsites with bare soil (own observation) which are important for the establishment of many plant species (Kotorová and Lepš, 1999; Münzbergová and Herben, 2005; Stammel et al., 2006; Fleischer et al., 2013).

Such early successional stages rich in bare soil are also known to favour the establishment of neophytes (Kowarik, 2010). At STOPON, however, neophytes rarely occurred (own observation). The most widespread neophyte was *Juncus tenuis* with constancy of 40%: its cover, however, was very low. All other observed neophytes had a much lower constancy and never formed dense stands. We assume that the combination of regular cutting and desludging with nutrient removal represses the establishment of dominance stands of these species.

Conductivity was higher at STOPON than at CONTROL within our study. Holtmann et al. (2018) previously showed that sodium and chloride concentrations are elevated at STOPON. A possible explanation for this is the run-off of de-icing salt from streets which cover larger areas in the surrounding of STOPON relative to CONTROL (Holtmann et al., 2017). However, despite these differences in conductivity, species density of salt-tolerating plants species did not differ between STOPON and CONTROL.

To summarise, species richness of aquatic, salt-tolerating aquatic and threatened plant species was generally high at STOPON and greater than that of CONTROL. The greater plant species richness of STOPON was driven by a higher habitat heterogeneity which was especially explained by (i) the genuine effect of habitat area on habitat heterogeneity, (ii) the existence of three similarly large habitat zones (terrestrial, semi-aquatic, aquatic) and (iii) the regular management, which represses shading plants, creates open soil and activates the soil seed bank. Due to the high species richness of threatened plant species such as *Centaurium pulchellum*, *Eleocharis palustris*, *Isolepis setacea*, *Myosotis laxa* or *Schoenoplectus tabernaemontani*, stormwater ponds play an important role for the conservation of plants in urban areas.

5. Implications for conservation

Currently, there are no fixed guidelines for the biodiversity-friendly construction and management of urban stormwater ponds. As a result, stormwater ponds differ considerably in the way they are constructed and managed, as well as in their environmental conditions between cities (own observation). The studied stormwater ponds in the city of Münster combine several attributes that are beneficial for the diversity of plant species (this study) and animal species (amphibians, odonates; Holtmann et al., 2017, 2018, 2019). Hence, they can serve, with some adjustments, as a blueprint for the construction and management of stormwater ponds in other cities.

As practised in the study area, soil application, planting or sowing of plants and paving or concreting of the banks should generally be omitted, although there is often a considerable public pressure to plant stormwater ponds. Additionally, stormwater ponds should be constructed to be large in overall size, with shallow slopes (proportion < 1:2) and three habitat zones (terrestrial, semi-aquatic and aquatic). Habitat heterogeneity within each of the three habitat zones can be enhanced by constructing the pond bed uneven with some depressions (e.g. Feldmann and Nöges, 2007; Sender, 2010). Cutting of the herb layer (every year) and woody riparian plants (every couple of years) as well as desludging of the ponds every couple of years should be performed in a mosaic-like manner and not, as currently applied in the study area, to the whole stormwater pond at once (Holtmann et al., 2017, 2018).

A few years after desludging, large parts of the semi-aquatic zone are often covered by dense carpets of the moss species *Calliergonella cuspidata* (own observation). Dense moss layers negatively affect germination of vascular plants (Kotorová and Lepš, 1999). In such stormwater ponds, additional soil disturbance with removal of the moss (e.g. by using a harrow) would be one possibility to foster successful vascular plant seedling establishment.

For the construction of new stormwater ponds especially, sites are relevant where hidden seed banks may exist (e.g. areas of former wet heathlands; Kaplan and Muer, 1990; Gee et al., 1997; Raabe and van de Weyer, 2005). Moreover, they should be constructed in connection with other small 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 plants would also benefit from a greater extent of ponds that are connected by semi-natural habitats (Snep et al., 2006; Gledhill et al., 2008; Willigalla and Fartmann, 2012; Holtmann et al., 2017, 2018).

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Appendix

Appendix A
Results of Spearman rank correlations (r_s). Only correlated variables are displayed. Variables with strong inter-correlations ($|r_s| \geq 0.5$) are highlighted by bold type. For further information cf. Section 2.2.2. Veg. height = Vegetation height of semi-aquatic herb layer, Sunshine = daily sunshine duration in June, ***$P < 0.001$.

	Terrestrial area	Semi-aquatic area	Aquatic area	Potassium	Phosphate	Nitrogen	Submerged aquatic plants	Reed bed	Riparian woodland	Veg. height	Sunshine	Water body heterogeneity
Plot size	**0.91*****	**0.72*****	**0.64*****	−0.37	−0.38	**−0.54*****	0.29	0.35	−0.49	0.36	**0.55*****	0.41
Terrestrial area	/	**0.57*****	0.49	−0.29	−0.31	−0.47	0.16	0.32	−0.45	0.31	**0.52*****	0.32
Semi-aquatic area	.	/	0.28	−0.29	−0.27	−0.44	0.25	0.46	−0.34	**0.57*****	0.37	0.30
Aquatic area	.	.	/	−0.39	−0.22	−0.21	0.23	0.43	−0.20	0.15	0.23	0.34
Potassium	.	.	.	/	**0.71*****	**0.50*****	−0.33	−0.15	0.40	−0.25	−0.44	−0.26
Phosphate	.	.	.	.	/	**0.81*****	−0.36	−0.22	0.44	−0.26	**−0.62*****	−0.28
Nitrogen	.	.	.	.	.	/	−0.38	−0.35	**0.56*****	−0.36	**−0.68*****	−0.34
Submerged aquatic plants	.	.	.	.	.	.	/	0.13	−0.24	0.02	0.33	**0.51*****
Reed bed	.	.	.	.	.	.	.	/	−0.34	0.46	0.50	**0.52*****
Riparian woodland	.	.	.	.	.	.	.	.	/	−0.35	**−0.62*****	−0.26
Veg. height	.	.	.	.	.	.	.	.	.	/	0.24	0.28
Sunshine	.	.	.	.	.	.	.	.	.	.	/	0.44

Appendix B

Statistics of GLM (single models): Relationship between plant species number and environmental parameters at stormwater ponds (STO) and control ponds (CON). Aqua = Aquatic plants, Salt = salt-tolerating aquatic plants, Threat = threatened plants. For further information cf. Section 2.2.2. – signifies negative relationship, + signifies positive relationship. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. not significant.

Parameter	STO	CON	STO	CON	STO	CON
	Aqua		Salt		Threat	
Area habitat zone						
Semi-aquatic	+**	n.s.	+***	n.s.	+**	n.s.
Aquatic	n.s.	+*	n.s.	n.s.	n.s.	n.s.
Soil type (baseline: sand)						
Silty sand	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Silty clay	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Aquatic zone						
Conductivity	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Depth	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Open soil	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.
pH value	n.s.	+*	n.s.	n.s.	n.s.	n.s.
Water level fluctuations	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Riparian woodland	−*	−***	−**	−***	n.s.	−*
Terrestrial and semi-aquatic zone						
Herb height terrestrial area	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Habitat heterogeneity (Shannon index)						
Plot heterogeneity	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Water body heterogeneity	+***	+**	+***	+**	+***	+**

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