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Effects of habitat and landscape quality on amphibian assemblages of urban stormwater ponds

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Abstract Urbanisation is one of the most severe drivers of current global biodiversity loss and has contributed to severe declines in many amphibian species. The aim of this study was to determine whether artificial stormwater ponds, designed to control water flow, can act as refuges for amphibians in urban areas. Moreover, we analysed the influence of habitat and landscape quality on amphibian species richness of 46 stormwater ponds (STOPON) in comparison to 46 control ponds (CONTROL).

Our study revealed that environmental conditions clearly varied between STOPON and CONTROL. The most pronounced differences were that STOPON were larger, shallower, sunnier, more isolated by streets and had a greater cover of built-up area and lower cover of arable land surrounding them. Nevertheless, the amphibian assemblages of STOPON and CONTROL were very similar. All nine amphibian species (including three threatened species) detected in this study were found in both pond types. Moreover, species richness (2.8 ± 0.2 vs. 2.3 ± 0.2) and the frequency of each species did not differ between STOPON and CONTROL. The only exception was *Pelophylax* spp., which occurred more regularly in STOPON. Both habitat and landscape quality affected amphibian species richness; however, the explanatory power of the habitat models was about twice as high as those of the landscape models.

In conclusion, stormwater ponds play an important role for amphibians in urban areas. In comparison to CONTROL, the low landscape quality in the surroundings of STOPON seemed to be compensated by a higher habitat quality due to regular management.

Keywords Aquatic connectivity · Fragmented landscape · Global change · Landscape structure · Retention pond · Species richness

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Introduction

Biodiversity loss is increasing at an alarming rate globally (Pimm et al. 1995; Barnosky et al. 2011; Naeem et al. 2012). For terrestrial biomes, land-use change has been identified as the main threat for the survival of species (Sala et al. 2000). Among land-use change, urbanisation is one of the most severe drivers of extinction (McKinney 2006; Grimm et al. 2008). The urban population is predicted to increase from 3.5 billion in 2010 to 6.3 billion in 2050 (United Nations 2010). Hence, urban areas are the fastest growing land-use type worldwide.

Urbanisation leads to a direct loss of natural and semi-natural habitats through building construction (Balmford et al. 2003; McKinney 2006; Steele and Heffernan 2014). Moreover, urbanisation dramatically alters the adjacent undeveloped areas. The size of the remaining habitat patches decreases while fragmentation increases (Lambin et al. 2001; Fahrig 2003; Donnelly and Marzluff 2006). Urban hydrosystems are heavily modified for both domestic and industrial use (Booth and Jackson 1997; Paul and Meyer 2001;

Hassall 2014; Hill et al. 2016). These alterations associated with urbanisation have a negative influence on the hydrologic balance and result in a higher runoff magnitude and an increase in flood frequency (Ehrenfeld 2000; Steele and Heffernan 2014).

To counteract the negative effects of urbanisation on the hydrologic balance, stormwater ponds have become more frequently constructed during 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 from other geographic regions indicate that stormwater ponds do not only fulfil a retention function but they also attract aquatic and semi-aquatic species (USA: Birx-Raybuck et al. 2010; Canada: Hassall and Anderson 2015; France: Scher and Thièry 2005; Le Viol et al. 2009; Le Viol et al. 2012; Australia: Hamer et al. 2012). However, for Central Europe there are virtually no studies on the conservation value of stormwater ponds in urban areas.

Very few animal groups are subject to a decline as severe as that of amphibians (Stuart et al. 2004; Beebee and Griffiths 2005). As many as one third of known amphibian species are considered as threatened (Wake and Vredenburg 2008; Barnosky et al. 2011). Although great attention has been paid to the widespread decline of amphibian populations due to man-made habitat loss, fragmentation and decrease in habitat quality for a long time (Wake 1991; Pechmann and Wilbur 1994; Alford et al. 2001), studies on the conservation value of artificial stormwater ponds for amphibians are rare (but see Brand and Snodgrass 2009).

Due to their complex bipartite life cycle with aquatic and terrestrial stages, amphibians are very sensitive to changes in both habitat and landscape quality (Collins and Storfer 2003; Stuart et al. 2004; Cushman 2006; Simon et al. 2009). Amphibians usually depend on aquatic spawning habitats, terrestrial summer feeding sites and hibernation habitats. The crucial parameters determining occurrence of amphibians are hydroperiod, water quality, vegetation structure, food availability and presence of predators, as well as landscape connectivity (Semlitsch 2008; Baldwin and deMaynadier 2009; Coster et al. 2014).

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

Material and methods

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.). Münster is located in north-western Germany, in the north of the Federal State of North Rhine-Westphalia close to the border of Lower Saxony (Fig. 1). The city has about 300,000 inhabitants and covers an area of 303 km^2 (City of Münster 2014). Of the total area, 34% are built-up areas and used for transport purposes; agricultural land covers 46%, forests 18% and water bodies 2%. Biogeographically, the city is part of the Westphalian Basin 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 2014).

Currently, 79 stormwater ponds exist in the study area (Möhring pers. comm.). Their banks are generally not paved or concreted and all ponds are regularly managed to ensure a maximum water retention volume. Management includes cutting of woody riparian plants every couple of years and of the herb layer usually every year during winter. Moreover, from time to time the ponds are desludged.

Sampling design

Amphibian assemblages

In this study, we examined 46 randomly selected stormwater ponds (STOPON) throughout the study area. Additionally, we surveyed the next pond (irrespective if it was a natural or artificial pond) in the vicinity of each STOPON (mean distance 816 m ± 23 m SE) as a control pond (CONTROL).

Amphibian assemblage surveys were carried out during the breeding period from March to May 2014. Each pond was surveyed four times, twice at night and twice during the day. Different methods were used due to the varying phenology and activity of each species (Glandt 2014). *Rana temporaria* was detected by spawn clumps during the day in mid-March (Jahn and Jahn 1997; Hachtel et al. 2009). Green frogs (*Pelophylax* kl. *esculentus, P. lessonae*, and *P. ridibundus*) were recorded during the day through visual and acoustic observation at the end of April. Due to the difficulties in identification, *Pelophylax* individuals were grouped as *Pelophylax* spp. for further analyses. However, whenever possible, individuals were caught with a dip net and an attempt was made to identify species to obtain at least general data on the presence and absence of the three green frog species at both studied pond types. As proposed by

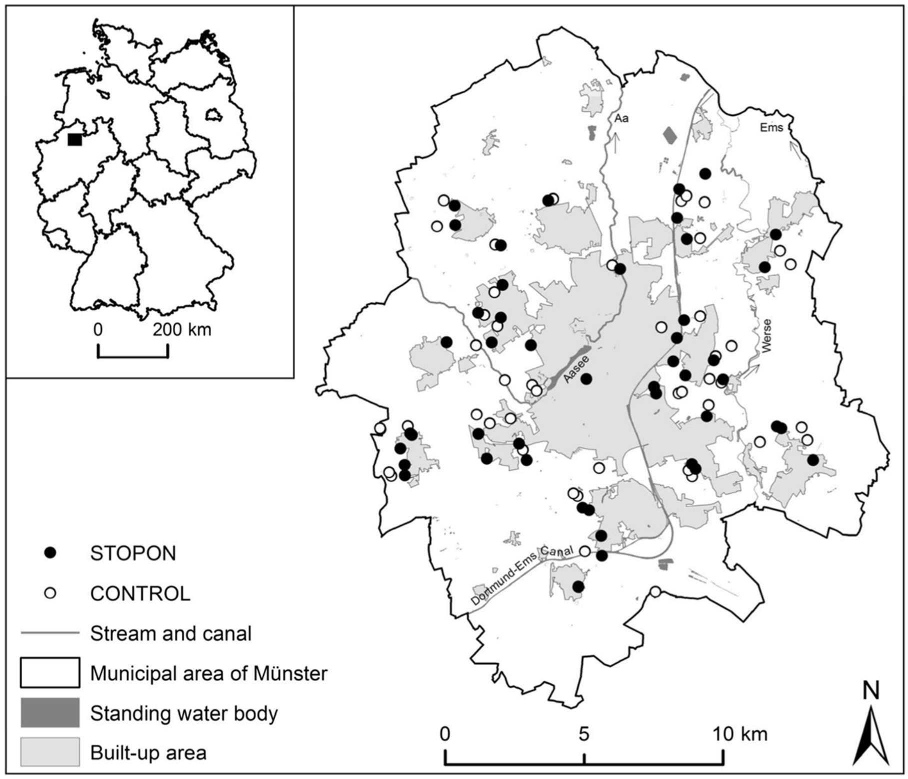

Fig. 1 Location of surveyed stormwater ponds (STOPON) and control ponds (CONTROL) in the municipal area of Münster (NW Germany)

Hachtel et al. (2009), the two night surveys were conducted between sunset and midnight. *Bufo bufo* and newt species (*Ichthyosaura alpestris, Lissotriton vulgaris,* and *Triturus cristatus*) were surveyed with a torch during the night at the end of March and the beginning of April (Hachtel et al. 2009). The use of traps to detect newts was discarded, as the risk of trap damage in urban areas is high (cf. Hartung et al. 1995; von Bülow 2014). *Hyla arborea* was detected by calling surveys during warm nights in May. Amphibian species were classified in the field according to Glandt (2011) and Tetzlaff (2007).

Habitat and landscape quality

For each studied pond we sampled several environmental parameters (Table 1). The water level fluctuations were measured during each survey. Occurrence of fish was sampled by visual inspection also during each survey. All other parameters that could not be derived from GIS calculations were recorded once between the end of April and the beginning of May. For spatial analyses we used ArcGIS 10.2 and aerial photographs. For each pond we calculated size and the mean distance to the next three ponds (geometric mean) to explain connectivity between ponds (Eichel and Fartmann 2008; Poniatowski and Fartmann 2010). Within a radius of 500 m around each pond we analysed landscape effects. In this way, we classified six different biotope types (woodland, grassland, arable land, settlement, urban green space, and water bodies) and calculated their cover. In addition, we considered isolation by streets in a radius of 100 m around each pond. For this purpose, streets were categorized into factor classes depending on their width (< 4 m: factor 0.01, 4–7 m: factor 0.1, > 7 m: factor 1) as a measure for traffic density (cf. Vos and Chardon 1998). This factor was multiplied by the percentage streets isolating the ponds, based on a maximum of four sides (no street = 0%, street at one side of the pond = 25%, streets at two sides of the pond = 50%, streets at three sides of the pond = 75%, streets at four sides of the pond = 100%). Finally, all determined products were summed to get the final isolation value:

$$\text{Isolation} = \sum\nolimits_{i=0.01}^{1} (\text{factor class for street width}_{\ i} \times \%\text{streets isolating the pond})$$

i could only take the values 0.01, 0.1 or 1. In case of two streets on one side of the pond only the broadest street was considered. To give an example, if a pond was surrounded by a street of 5 m width at one side and a street of 8 m width at another side, the isolation was calculated as follows: 0.1 × 25 + 1 × 25 = 27.5%.

Table 1 Overview of sampled predictor parameters (mean values ± Standard Error [SE], minimum and maximum) and their analysis in Generalized Linear Models (GLM). Spearman rank correlation coefficients (r_s) were calculated for all pairs of predictor variables. If two or more were strongly intercorrelated ($|r_s| > 0.6$) only the most important (biologically-relevant) variable was used. 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 pond types are indicated by bold type: n.s. = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Parameter	Correlation			STOPON		CONTROL		P
	r_s		Used variable	Mean ± SE	Min.–Max.	Mean ± SE	Min.–Max	
Habitat level								
Structural parameters								
Size (m²) [a]	.		.	2629 ± 435	52–16,874	812 ± 195	18–8243	$\boldsymbol{W}^{***}$
Depth (cm)	−0.74	>	Shallow water	37.9 ± 4.2	2–126	51.6 ± 3.4	15–145	$\boldsymbol{t}^{*}$
Shallow water (%) [b]	1.00			77.0 ± 4.9	5–100	46.6 ± 5.0	5–100	$\boldsymbol{W}^{***}$
Water level fluctuation (cm) [c]	.		.	7.7 ± 1.3	0–55	10.2 ± 0.8	0–21	$\boldsymbol{W}^{**}$
Bank inclination (°) [d, e]	.		.	16.3 ± 1.3	8–40	19.0 ± 2.2	2–70	$W^{n.s.}$
Conductivity (μS/cm) [f]	.		.	690.9 ± 318.4	140–1290	505.4 ± 295.4	96–1495	$\boldsymbol{W}^{**}$
Vegetation cover (%)								
Open water surface	−0.97	>	Total vegetation cover	61.7 ± 4.6	0–100	66.5 ± 4.7	0–100	$t^{n.s.}$
Total vegetation cover	0.97			51.4 ± 5.0	0–100	44.2 ± 5.6	0–100	$\boldsymbol{W}^{**}$
Reed bed	0.73			27.3 ± 4.3	0–100	16.3 ± 2.8	0–60	$W^{n.s.}$
Algae	.		.	7.8 ± 2.1	0–65	4.7 ± 1.4	0–35	$W^{n.s.}$
Floating aquatic plants	.		.	7.0 ± 2.6	0–75	15.4 ± 4.1	0–100	$W^{n.s.}$
Submerged aquatic plants	.		.	9.3 ± 2.3	0–60	10.5 ± 2.8	0–95	$W^{n.s.}$
Riparian woodland	1.00	>	Riparian woodland	42.3 ± 5.1	0–100	57.9 ± 4.2	0–100	$\boldsymbol{t}^{*}$
Daily sunshine duration (h) [d, g]								
April	−0.62			7.3 ± 0.6	0.4–14.0	4.0 ± 0.5	0.0–13.5	$\boldsymbol{t}^{***}$
Landscape level								
Land cover (%) [a]								
Grassland	.		.	8.8 ± 1.6	0–64	11.5 ± 1.4	0–58	$t^{n.s.}$
Woodland	.		.	12.0 ± 1.3	0–30	19.3 ± 2.1	0–55	$\boldsymbol{W}^{**}$
Arable land	−0.78	>	Built-up area	30.2 ± 2.7	0–63	45.3 ± 3.1	0–78	$\boldsymbol{t}^{***}$
Built-up area	1.00			44.4 ± 2.8	5–95	20.4 ± 3.0	0–85	$\boldsymbol{t}^{***}$
Urban green space	.		.	2.3 ± 0.7	0–24	1.6 ± 0.5	0–15	$W^{n.s.}$
Water bodies	.		.	2.3 ± 0.5	0–15	2.0 ± 0.4	0–10	$W^{n.s.}$
Connectivity								
Distance to next three ponds (m) [a, h]	.		.	341.5 ± 28.9	28–973	264.1 ± 25.8	26–865	$W^{n.s.}$
Isolation by streets (%) [a]	.		.	18.2 ± 2.2	0–52.5	8.9 ± 3.1	0–100	$\boldsymbol{W}^{***}$

[a] Calculated from aerial photographs by using ArcGIS 10.2

[b] Water depth: < 30 cm

[c] Measured by using a water gauge

[d] Mean of four measures at N, E, S, W

[e] Measured by using a compass with inclinometer

[f] Measured by using a multi-parameter probe (Hanna HI 98129)

[g] Measured by using a horizontoscope after Tonne (1954)

[h] Geometric mean

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 paired *t* test, if data were normally distributed; otherwise a Wilcoxon *Z* test was conducted. Differences in nominal variables were tested using Chi^2 test.

Prior to multivariate analyses, spearman rank correlations (r_s) were conducted to exclude variables with strong intercorrelations ($|r_s| \geq 0.6$). All remaining parameters (Table 1) were included in the analyses described below. A Principal Component Analysis (PCA) was done to assess the relationships between environmental parameters and pond types.

To evaluate the influence of habitat and landscape quality on species richness, we applied Generalized Linear Models (GLM). On the habitat level we conducted a GLM for each environmental parameter to reduce the number of predictor variables (Appendix Table 5). To avoid over-fitting, only significant parameters were integrated into a habitat model. At the landscape level, the number of predictor variables was much lower. Consequently, all variables were integrated into a landscape model. Finally, all significant variables of the habitat level and landscape level model were incorporated in a synthesis model.

The analyses were performed using Canoco 5.01, R-3.2.2 (R Development Core Team 2016), SigmaPlot 13.0 and IBM SPSS Statistics 23.

Results

Environmental parameters

CONTROL were mostly located in rural areas, while STOPON were predominantly situated in the suburbs (Fig. 1). Most of the environmental parameters differed significantly between STOPON and CONTROL (Table 1). At the habitat level, STOPON were larger and shallower. Moreover, water levels fluctuated more strongly, conductivity and total vegetation cover were higher while the cover of riparian woodland was lower in STOPON. Due to this latter fact, the sunshine duration in April was higher. The remaining numerical environmental parameters did not differ between STOPON and CONTROL.

The vast majority of the studied ponds ($N = 72$, 66%) were permanent ponds without fish (Table 2). Both the presence of fish and hydroperiod did not differ between STOPON and CONTROL.

At the landscape level, the cover of the built-up area and the isolation by streets were greater in the area surrounding the STOPON than at those surrounding the CONTROL (Table 1). In contrast, woodland and arable land cover was lower. The strong differences in environmental conditions between the two pond types are confirmed by the PCA, which shows a clear separation of CONTROL and STOPON along the first axis (Fig. 2, Table 3).

Amphibian species assemblages

Species richness

A total of nine amphibian species (three urodelans, six anurans) were detected in the 92 investigated ponds (Fig. 3). All species occurred in both STOPON and CONTROL. Three species (*Hyla arborea*, *Pelophylax lessonae*, and *Triturus cristatus*) are listed in the red data book of North-Rhine Westphalia (LANUV NRW 2011). Species richness did not differ between the two pond types (STOPON: 2.8 ± 0.2 vs. CONTROL: 2.3 ± 0.2; Wilcoxon signed rank test, $W = -218.0$, $P = 0.11$). The three most frequent species were *Pelophylax* spp., *Rana temporaria* and *Bufo bufo* (Fig. 3). They occurred in at least 50% of each of the two pond types. Significant differences in absolute frequencies were only observed in *Pelophylax* spp., which occurred more regularly in the STOPON.

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 Chi^2 test. n.s. = not significant

Parameter	STOPON		CONTROL		P
	N	%	N	%	
Fish					n.s.
Present	3	6.5	2	4.3	
Absent	43	93.5	44	95.7	
Hydroperiod					n.s.
Permanent	36	78.3	41	89.1	
Temporary	10	21.7	5	10.9	

Effects of habitat and landscape quality on amphibian species assemblages

Both habitat and landscape quality affected amphibian species richness in the studied ponds (Table 4). In the STOPON species richness was highest in permanent ponds. Species richness increased with rising algae cover and decreasing cover of riparian woodlands and built-up areas in the landscape surrounding the ponds. Generally, the explanatory power of the models was high (McFadden Pseudo-R^2: 0.19–0.42).

In the CONTROL submerged aquatic plants had a positive relationship (habitat model) and isolation by streets had a negative relationship (landscape model) with species richness. However, the explanatory power of both models was low (McFadden Pseudo-R^2: 0.06 and 0.13, respectively) and the synthesis model failed to even identify significant predictors of species richness.

Generally, the explanatory power of the habitat models was about twice as high as those of the landscape models.

Discussion

Our study revealed that environmental conditions clearly varied between the STOPON and CONTROL. The most

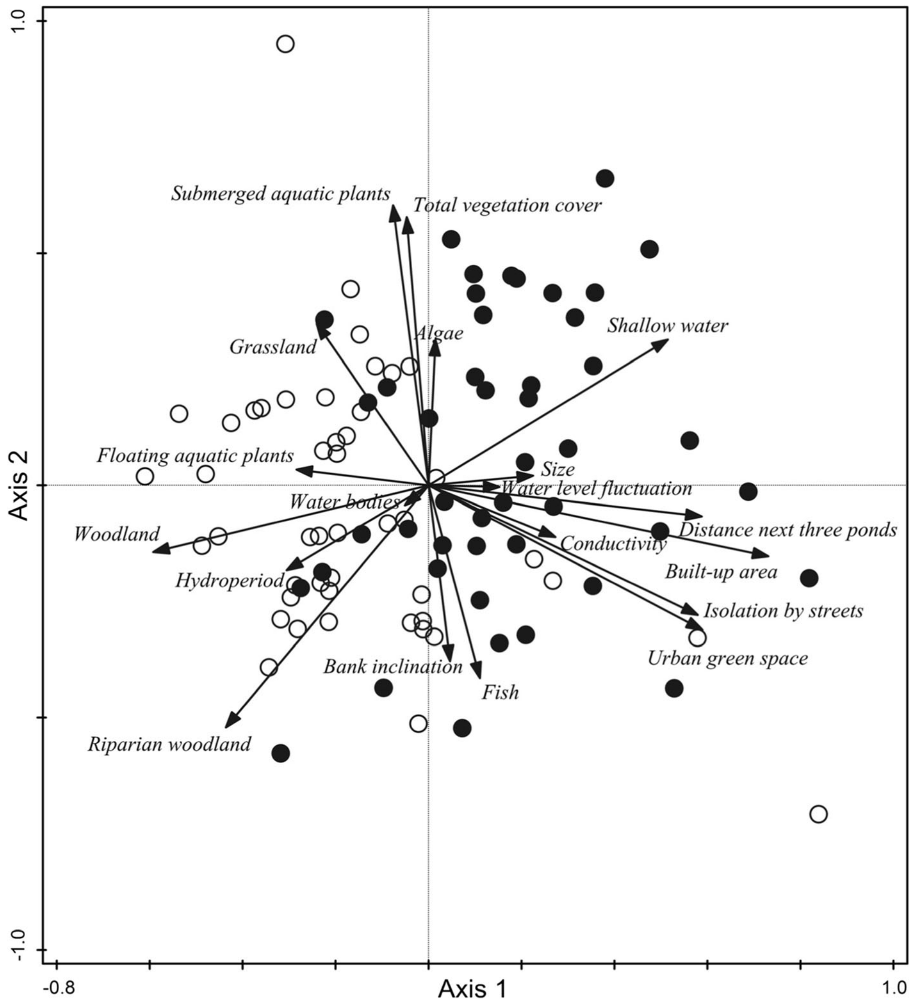

Fig. 2 Principal Component Analysis (PCA) biplot based on the two pond types and sampled environmental parameters. Filled circles = stormwater ponds, empty circles = control ponds

pronounced differences were that STOPON were larger, shallower, sunnier, more isolated by streets and had a greater cover of built-up area and lower cover of arable land surrounding them. Nevertheless, the amphibian assemblages in the STOPON and CONTROL were very similar. All nine amphibian species (including three threatened species) detected in this study were found in both pond types. Moreover, species richness and the frequency of each species did not differ between STOPON and CONTROL. The only exception was *Pelophylax* spp., which occurred more frequently in the STOPON. Both habitat and landscape quality affected amphibian species richness. However, the explanatory power of the habitat models was about twice as high as those of the landscape models.

The nine amphibian species detected in this study comprise 82% of the current amphibian fauna of the municipal area of Münster, which consists of eleven species (cf. Hachtel et al. 2011). Both absent species (*Bufo calamita*, *Salamandra salamandra*) are very localised in the study area, occurring far away from the studied ponds (pers. obs.). Consequently, all possible amphibian species were detected in the two pond types.

The explanatory power of the models was high for STOPON (McFadden Pseudo-R^2: 0.19–0.42), suggesting that the important drivers of amphibian species richness in urban stormwater ponds were recorded. In contrast, the CONTROL model accuracy was low (McFadden Pseudo-R^2: 0.06 and 0.13) and the synthesis model even failed to identify significant predictors. Hence, the results for CONTROL allow only limited interpretations of the drivers of species richness. However, this is of minor importance as the focus of this study was on the parameters that explain amphibian species richness in stormwater ponds.

The explanatory power of the models did not only differ between the two pond types but also between the spatial levels. McFadden Pseudo-R^2 values for both STOPON and CONTROL were about twice as high at the habitat level than at the landscape level. This is in line with other studies that also identified habitat quality to be more important for amphibians than landscape quality (Vági et al. 2013; Jeliazkov et al. 2014).

At the habitat level, we determined hydroperiod, cover of algae and riparian woodland (all at STOPON), as well as cover of submerged aquatic plants (CONTROL) as predictors

Table 3 Summary of PCA (explained variance and Pearson correlations) based on the two pond types and environmental parameters. n.s. = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Parameter	Axis 1	Axis 2
Habitat level		
Structural parameters		
Size	0.22$^{n.s.}$	0.02$^{n.s.}$
Shallow water	0.52***	0.31**
Water level fluctuation	0.15$^{n.s.}$	0.00$^{n.s.}$
Bank inclination	0.05$^{n.s.}$	−0.38***
Conductivity	0.27**	−0.11$^{n.s.}$
Fish	0.11$^{n.s.}$	−0.41***
Hydroperiod	−0.31**	−0.18 $^{n.s.}$
Vegetation cover		
Total vegetation cover	−0.08$^{n.s.}$	0.60***
Algae	0.01$^{n.s.}$	0.31**
Floating aquatic plants	−0.28**	0.03$^{n.s.}$
Submerged aquatic vegetation	−0.05$^{n.s.}$	0.58***
Riparian woodland	−0.44***	−0.52***
Landscape level		
Land cover		
Grassland	−0.24*	0.35**
Woodland	−0.59***	−0.14$^{n.s.}$
Built-up area	0.73***	−0.15$^{n.s.}$
Urban green space	0.59***	−0.31**
Water bodies	−0.05$^{n.s.}$	−0.04$^{n.s.}$
Connectivity		
Distance next three ponds	0.59***	−0.07$^{n.s.}$
Isolation by streets	0.58***	−0.28**
Explained variance (cumulative)	14.4	26.1

of amphibian species richness. High species richness was found in permanent ponds. This is in contrast to other studies that emphasised the importance of temporary water bodies as breeding sites for amphibians (e.g., Ficetola and De Bernardi 2004; Vági et al. 2013). Temporary water bodies tend to lack larger predators, especially fish, which can explain the amphibian species richness. However, in our study fish occurrence was generally negligible in both pond types. Additionally, temporary ponds only harbour species-rich amphibian assemblages if the dry period is not too long during the spawning season and the period of larvae development (Günther 2009). Most of the temporary STOPON ponds were already dried-up by late spring and early summer (pers. obs.). In addition, species adapted to develop in temporary ponds (even those only filled with water for very short time periods) are generally missing in the wider study area (e.g., *Bombina variegata*) (Hachtel et al. 2011) or occur in very localised remote areas of the study area (*Bufo calamita*, see above).

There is clear evidence that a certain amount of aquatic vegetation is generally important for species-rich amphibian assemblages (Günther 2009; Kret and Poirazidis 2015) and that species richness is related to the complexity of the aquatic vegetation (Hamer and Parris 2011). This is especially true for water bodies where the cover of aquatic vegetation is low, as was the case in most of our studied ponds. Heterogeneous vegetation provides suitable substrates for spawning (Tóth et al. 2011) and offers hiding places to escape from predators (Morgan and Buttemer 1996; Baber and Babbitt 2004). Moreover, for anurans leaves of floating aquatic plants are used for sun basking as well as to ambush prey and to detect potential predators (Günther 2009). Surprisingly, amphibian species richness did not only increase with the cover of submerged aquatic plants (CONTROL) but

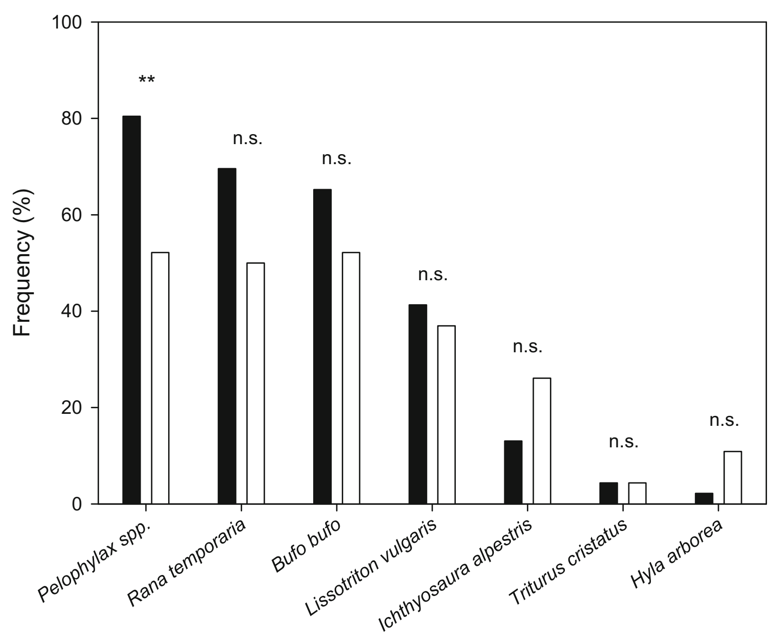

Fig. 3 Frequencies of amphibian species in stormwater (black) and control ponds (white). *Pelophylax* spp.: The dominant species was *P.* kl. *esculentus*, which occurred in all ponds where *Pelophylax* spp. was present. However, we found *P. lessonae* at two stormwater ponds and three control ponds as well as *P. ridibundus* at 18 and 10, respectively. Differences in absolute frequencies were tested by likelihood Chi^2 test. n.s. = not significant, ** $P < 0.01$

Table 4 Statistics of GLM: Relationship between species number and environmental parameters of stormwater ponds (STOPON) and control ponds (CONTROL), respectively. 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 categorical predictors and the intercepts were analysed using Wald tests. STOPON by Gaussian and CONTROL by poisson error structure, respectively. n.s. = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. R^2_{MF} = Pseudo-R^2 [McFadden]

STOPON				CONTROL			
Parameter	Estimate	SE	P	Parameter	Estimate	SE	P
Habitat model (R^2_{MF} = 0.32)				*Habitat model (R^2_{MF} = 0.13)*			
Intercept	3.363	0.363	***	Intercept	2.210	0.269	***
Hydroperiod (baseline: permanent)			*	Submerged aquatic plants	0.022	0.012	*
Temporary	−1.167	0.437	*				
Algae	0.024	0.013	*				
Riparian woodland	−0.013	0.005	*				
Landscape model (R^2_{MF} = 0.19)				*Landscape model (R^2_{MF} = 0.06)*			
Intercept	4.153	0.467	***	Intercept	0.916	0.103	***
Built-up area	−0.031	0.010	**	Isolation by streets	−0.010	0.006	*
Synthesis model (R^2_{MF} = 0.42)				*Synthesis model*			
Intercept	4.269	0.491	***	n.s.			
Hydroperiod (baseline: permanent)			*				
Temporary	−0.794	0.435	*				
Algae	0.024	0.013	*				
Riparian woodland	−0.012	0.005	*				
Built-up area	−0.023	0.009	*				

also with the cover of algae (STOPON), which is usually interpreted as an indicator of eutrophication if algae from dense carpets (Uhlmann and Horn 2001). However, the mean cover of algae was very low at STOPON (8%, Table 1). There are two possible explanations why amphibian species richness was correlated with algae cover at STOPON: (i) Low algae cover increases the structural complexity of sparsely-vegetated water bodies, which has beneficial effects on amphibians, as explained before. (ii) Algae serve as food for the larvae of anurans, which enhances their development and survival (Vági et al. 2013).

Several studies showed that pond shading negatively affects amphibian species assemblages (Skelly et al. 1999; Werner and Glennemeier 1999; Hamer and Parris 2011; Kret and Poirazidis 2015). This is due to reduced light and water temperatures resulting in fewer food resources for larvae (e.g., periphyton), which impedes larval growth and survival. Indeed, shading of ponds was also an important driver of amphibian species richness in the STOPON. Amphibian diversity was negatively correlated with the cover of riparian woodland, which was negatively correlated with sunshine duration in April.

At the landscape level, amphibians responded negatively to urbanisation, namely to built-up areas in the area surrounding their breeding habitats (STOPON) and isolation by streets (CONTROL). An increase in built-up areas and streets due to urbanisation results in a direct loss of natural and semi-natural habitats for wildlife. Indirectly, habitat connectivity decreases and the remaining habitat patches become isolated (Hamer and McDonnell 2008). This is especially true for amphibians that (i) exhibit metapopulation structures and (ii) depend on migration corridors between breeding ponds and terrestrial habitats (Marsh and Trenham 2001). STOPON are mainly situated in the suburbs (this study, Willigalla and Fartmann 2012), where natural and semi-natural habitats that could be potential migration corridors and terrestrial habitats are very limited (cf. Table 1), which explains why species richness decreased with increasing cover of built-up areas. Streets affect amphibians in two ways: (i) Directly by killing individuals due to traffic and (ii) indirectly by habitat fragmentation (Hels and Buchwald 2001). The increased isolation by roads hinders the exchange of individuals between habitat patches, resulting in reduced genetic diversity (Reh and Seitz 1990; Vos and Chardon 1998). As a consequence, the interacting effects of both threats lead to an increased extinction risk of populations.

Although STOPON were, at the landscape level, more strongly affected by urbanisation (greater cover of built-up area and greater isolation by streets), they had very similar amphibian assemblages compared to CONTROL. For *Pelophylax* spp. there was even a positive relationship with STOPON. We assume that the low landscape quality in the surroundings of STOPON was compensated by a higher habitat quality. STOPON were shallower und sunnier than CONTROL, which generally favoured amphibian species richness (see above). The high sunshine duration at STOPON is the result of regular cutting of the riparian trees to guarantee maximum water retention (Möhring pers. comm.). In contrast, management of CONTROL was usually lacking (pers. obs.) and hence, the ponds were often surrounded by riparian woodland.

Pelophylax species are known to prefer sunny and nutrient-rich water bodies (Günther 2009). Both conditions are fulfilled by STOPON. Additionally, *Pelophylax* species are, throughout their whole lifetime, more strongly associated with water bodies than most other amphibian species (Günther 2009). Due to this reduced use of terrestrial habitats they seem to be less sensitive to the effects of urbanisation at the landscape level.

In conclusion, our study showed that stormwater ponds play an important role for amphibians in urban areas. Generally, habitat quality was more important than landscape quality for amphibian species richness in the studied ponds. Although STOPON were, at the landscape level, more strongly affected by urbanisation, they had very similar amphibian assemblages compared to CONTROL. One species, *Pelophylax* spp., even occurred more regularly at STOPON due to a more favourable habitat quality for this species group. The low landscape quality in the area surrounding the STOPON seemed to be compensated by a higher habitat quality in comparison to CONTROL.

Implications for conservation

This study shows that stormwater ponds have a great value for amphibians in urban areas, especially due to a relatively high habitat quality. The regular management of the stormwater ponds leads to a low cover of riparian woodland and, hence, a high sunshine duration, which together with large areas of shallow water, favour amphibians.

Despite the generally positive evaluation of current stormwater pond management in the study area there are possibilities for optimisation. Species richness was lowest in temporary stormwater ponds. A lack of structural complexity in the water bodies and shading were further parameters that limited species numbers. Consequently, temporary stormwater ponds should be reconstructed to permanent ponds, preferentially comprising of large areas of shallow water. Vegetation heterogeneity within the water bodies can be enhanced, if cutting of the aquatic vegetation and desludging was performed in a mosaic-like manner from year to year and not, as currently applied, to the whole stormwater pond at once. Additionally, at less sunlit ponds shading trees should partly be removed.

Dense networks of ponds and semi-natural habitats are generally known to support amphibian populations (Jeliazkov et al. 2014) by facilitating dispersal (Hamer and Parris 2011) and increasing the availability of suitable breeding sites. This is particularly true in urban environments where large built-up areas that, as shown by our study, negatively affect amphibian species richness of stormwater ponds by reducing connectivity. Consequently, we recommend enhancing connectivity between stormwater ponds through the creation of urban green space and the creation of new ponds along such potential dispersal corridors. Taxa other than amphibians 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).

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Appendix 1

Table 5 Statistics of single GLM (estimates ± SE) at the habitat level: Relationship between species number and all environmental parameters in stormwater ponds (STOPON, Gaussian error structure) and control ponds (CONTROL, Poisson error structure), respectively. n.s. = not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Parameter	STOPON			CONTROL		
	Estimate	SE	P	Estimate	SE	P
Structural parameters						
Size	0.000	0.000	n.s.	0.000	0.000	n.s.
Water level fluctuation	−0.014	0.023	n.s.	0.010	0.017	n.s.
Bank inclination	−0.018	0.023	n.s.	−0.003	0.007	n.s.
Conductivity	−0.001	0.001	n.s.	0.000	0.000	n.s.
Fish (baseline: present)						
Absent	−0.256	0.826	n.s.	0.455	0.586	n.s.
Hydroperiod (baseline: permanent)						
Temporary	1.100	0.466	*	−0.719	0.420	n.s.
Vegetation cover (%)						
Total vegetation cover	−0.018	0.213	n.s.	0.127	0.093	n.s.

Table 5 (continued)

Parameter	STOPON			CONTROL		
	Estimate	SE	P	Estimate	SE	P
Algae	0.039	0.014	**	0.013	0.009	n.s.
Floating aquatic plants	0.008	0.012	n.s.	−0.004	0.004	n.s.
Riparian woodland	−0.013	0.006	*	0.001	0.003	n.s.
Submerged aquatic plants	0.023	0.013	n.s.	0.009	0.004	*
Shallow water	−0.008	0.006	n.s.	−0.006	0.003	n.s.

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