

Urbanization affects frog communities at multiple scales in a rapidly developing African city

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Abstract Urbanization is worldwide among the biggest threats to amphibian populations. However, hardly any studies have been conducted on the effects thereof in developing countries. Amphibian distribution and community assemblages are not well understood in aquatic and terrestrial habitats that are rapidly changing due to human modification. We conducted four surveys using three detection methods for both anuran larvae and predatory fish in 61 ponds in and around the city of Potchefstroom, South Africa. Tadpoles of eight anuran species and seven fish species were detected during the field surveys. The common river frog (*Amietia queckettii*) was the most abundant species, occurring in 39 % of the sites, whereas the bubbling kassina (*Kassina senegalensis*) was detected in only one pond. The remaining six species were detected in 6.6–26.2 % of the sites. Predatory fish were detected in 64 % of the wetlands with mosquitofish (*Gambusia affinis*) and the banded tilapia (*Tilapia sarrmanii*) detected respectively in 44 and 43 % of the sites. High species richness was associated with well-vegetated wetlands, low urban CBD surface area and conductivity, large pond areas and steeper bank slopes. Conductivity and pH showed only weak negative effects on species richness. This is the first study to quantify the effects of urbanization on frog communities in a developing city on the African continent. Our results demonstrate that both local and landscape variables affect amphibians in a small but rapidly developing city. Accordingly, management practices need to adopt a multi-scale approach if we are to conserve amphibians in African cities.

Keywords Anuran habitat · Indirect gradient analysis · Landscape · Predatory fish · Urbanization

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Introduction

Urbanization is among the biggest threats to amphibian populations worldwide (Czech et al. 2000; Marzluff 2001; Stuart et al. 2004; Beebee and Griffiths 2005; Cushman 2006; Hamer and McDonnell 2008; Measey and Tolley 2011; Mokhatla et al. 2012). No less than 88 % of threatened amphibians are impacted by urbanization through habitat loss, fragmentation and degradation (Baillie et al. 2004). The life history stages of amphibians necessitates a multi-spatial approach when defining habitat, for as the name amphibian suggests (*amphi* = two/both + *bios* = life/living), these animals require both suitable aquatic habitat to breed and metamorphose from free-swimming larval stages, as well as terrestrial habitat to mature, forage and hibernate (Pope et al. 2000; Semlitsch and Bodie 2003; Cushman 2006; Pillsbury and Miller 2008; Lemckert et al. 2012). Therefore, urbanization can affect amphibians at a local micro-habitat level by changing water quality and surface hydrology (Pechmann et al. 1989; Vershinin and Tereshin 1999; Babbitt and Tanner 2000) as well as at larger landscape scales by altering and fragmenting habitat, and creating movement barriers that lead to the loss of metapopulation connectivity (Hager 1998; Vos and Chardon 1998; Houlihan and Findlay 2003; Semlitsch and Bodie 2003; Rothermel 2004; Trenham and Shaffer 2005; Hamer et al. 2008; Heard et al. 2013). Although habitat alteration, degradation and fragmentation have a more direct effect on anurans, urbanization can also affect anurans indirectly via changes in acoustic environments (Sun and Narins 2005; Parris et al. 2009; Narins 2013), changes in urban atmospheric conditions (Narins and Meenderink 2014) as well via the attitudes of people towards frogs that can affect the persistence and success of anuran populations (Ceriaco 2012). In this paper we will only focus on the effects of urbanization pertaining to habitat change.

On a landscape scale, vast amounts of surface area are altered by replacing natural habitat with impervious surfaces associated with business districts, industrial, residential and agricultural landscapes, leaving only fragments of terrestrial and aquatic habitats that are transformed and, in worse cases, completely overbuilt. The built environment creates multiple barriers via roads, houses and walls or fences, leaving anurans with challenging and in most cases impossible migration routes that weaken or totally block ecological connectivity between wetlands and dispersal habitat (Vos and Chardon 1998). Studies have frequently shown a negative correlation between species richness and urban density (Findlay and Houlihan 1997; Pillsbury and Miller 2008; Hamer and Parris 2011). Urban landscapes can be defined by almost decomposable, nested spatial hierarchies, in which hierarchical levels correspond to structural and functional units functioning at distinct spatial and temporal scales (Reynolds and Wu 1999; Wu and David 2002; Alberti 2008). The different spatial and hierarchical units of the landscape vary with socioeconomic and biophysical processes, i.e., from households and buildings to habitat patches or remnant ecosystems (Alberti 2008). Therefore, it is necessary to understand the underlying community dynamics of anurans within this complex network of an altered environment.

Urbanization has a profound effect on predation in water bodies through the introduction of invasive fish species (Pilliod et al. 2012). Predation on tadpoles and eggs by fish decreases amphibian survival, and subsequently reduces species richness and occurrence in urban areas (Ficetola and De Bernardi 2004; Pearl et al. 2005; Hamer and Parris 2011, 2013). Along with hydroperiod, predation has the potential to alter the structure of larval amphibian communities (Wellborn et al. 1996; Hamer and Parris 2013). Even low densities of invasive fish species may have detrimental effects on native amphibians (Lydeard and Belk 1993; Pilliod et al. 2012). Globally, several species have been shown to have adverse effects on amphibian populations. These include poeciliids (mosquitofish), salmonids (trout and bass) and cyprinids (carps) (Formas 1995; Gillespie and Hero 1999), and odontobutid (Rotan) (Pilliod et al. 2012). Two

mosquitofish species (*Gambusia affinis* and *G. holbrooki*), that are native to southern and eastern United States, now have global distributions due to their former popularity as biological control agents for mosquito larvae (Courtenay and Meffe 1989). They are small and effective aquatic predators and have been considered a major driver for native fish and amphibian declines in Australia, New Zealand and the Western United States (Bence 1988; Courtenay and Meffe 1989; Lydeard and Belk 1993; Mahony 1999; Komak and Crossland 2000; Hamer et al. 2002; Hamer and Parris 2013).

To sustain biodiversity within urban landscapes, features that support local amphibian populations must be identified (Scheffers and Paszkowski 2013). Hazell et al. (2004) demonstrated that both natural and constructed ponds in agricultural landscapes have a part to play in conservation of anuran diversity and providing habitat for frogs, provided that heterogeneity in waterbody characteristics across the landscape is preserved. Studies have shown that landscape determinants that play a role promoting urban anuran diversity include larger areas of green open space for metapopulation connectivity and provision of terrestrial foraging habitat, (Hazell et al. 2004; Hamer and Parris 2011; Scheffers and Paszkowski 2013). At the landscape scale, roads and road traffic can have profoundly negative impacts on amphibian communities in urban areas (Eigenbrod et al. 2009; Mokhatla et al. 2012; Beebee 2013).

The perseverance of anuran populations in urban landscapes has been shown to depend on variables at different spatial scales, from individual breeding sites to larger landscapes that may extend for kilometers beyond a pond (Pellet et al. 2004a, 2004b; Drinnan 2005; Rubbo and Kiesecker 2005; Pillsbury and Miller 2008; Hamer and Parris 2011). Very few studies report how anuran communities as a whole respond to urbanization at both local (micro-habitat) and landscape scales (Pillsbury and Miller 2008; Hamer and Parris 2011). This study is the first to assess the effects of urbanization on anuran communities as a whole on a multi-spatial scale in the African continent (but see Measey and Tolley 2011; Mokhatla et al. 2012). The aim of this study was to assess anuran community assemblages along an indirect urban–rural gradient in Potchefstroom, South Africa, and determine which micro-habitat and landscape variables relating to urbanization influence the distribution of the regional amphibian community.

Materials and methods

Study area

Potchefstroom is an academic city located in the North-West Province, South Africa and about 120 km west-southwest of Johannesburg. It hosts the Potchefstroom Campus of the North-West University. The city is one of the oldest in northern South Africa and has a rich history with the first European people settling in 1838 (Badenhorst et al. 1939; Jenkins 1971). Although Potchefstroom is one of the oldest towns in the country, it has not developed into a large city such as Cape Town and Johannesburg. It is a multi-cultural town of 2 573 km², populated by more than 162 700 residents. There was a 2.4 % population increase reported in the decade spanning from 2001 to 2011. This is a 1.8 % increase on the previous decade and 0.8 % higher than that of the North-West Province as a whole for the same period (Tlokwe City Council 2011). This underscores the potential exponential future growth rate for this developing city.

Potchefstroom is located close to the Vredefort Dome world heritage site, the oldest and largest reported astrobleme (an eroded remnant of a large crater made by the impact of a meteorite) globally (McCarthy and Rubridge 2005; Norman and Whitfield 2006). The geological alterations that formed from the impact 190 million years ago brought about a relatively rich faunal and floral diversity within the Grassland and Savanna biomes (Mucina and

Rutherford 2006). Within the Tlokwe City Council Municipality there are three threatened terrestrial ecosystems covering more than 13 % of the district area, and contains 401 wetlands covering 3 664 ha (SANBI 2009).

Site selection for larval amphibian and fish survey

A pilot survey on 104 wetlands (i.e., water bodies) was conducted between 1 February and 14 April 2012 in order to evaluate physical properties of sites to be selected for primary surveys. Taking time- and man-power constraints into consideration, 68 wetlands were randomly selected using the RANDOM function in Microsoft Office Excel 2010 and divided into nine wetland-type categories namely: roadside pools ($n=6$), formal ornamental ponds ($n=12$), garden ponds ($n=12$), permanent rivers ($n=6$), former quarries ($n=4$), small farm dams $<50\,000\text{ m}^2$ ($n=6$), big dams $>100\,000\text{ m}^2$ ($n=6$), vlei (low-lying, marshy ground with prominent reed and sedge vegetation cover) ($n=7$), and large peri-urban ponds ($n=9$). The availability of 68 wetlands for sampling was further reduced to 61 sites by drought conditions as seven sites were dry for the entire duration of the study (Online Resource: see Table A1 for site descriptions).

Four aquatic surveys at the 61 selected wetland sites were conducted during autumn, spring, and summer: 1) 8 May - 28 May 2012, 2) 10 September - 30 September 2012; 3) 14 November - 4 December 2012, and 4) 19 January - 8 February 2013. The study was designed to include the breeding and larval development periods of all 11 species occurring in the region (Du Preez and Carruthers 2009). During the four surveys it was assumed that the wetlands were closed to local colonization and or extinction by frogs. The sequence in which wetlands were visited was randomized.

Detection methods

Three techniques were used simultaneously for aquatic sampling of amphibian larvae and fish: electro-fishing, bottle trapping and dip-netting (Online Resource: see Table A2 for list of wetland effort quantification). Electro-fishing were carried out with a backpack electro-fisher (SAMUS725M) which was used to collect fish and tadpoles prior to using the other two techniques at a site. Stunned fish and startled tadpoles were collected with a landing net (2.5 mm mesh and square frame, $300\times 300\text{ mm}$) and placed into buckets (separate buckets for tadpoles and fish). To standardize sampling effort, the total amount of time spent electro-fishing was relative to the surface area of a wetland (2 min minimum, plus one additional minute per doubling of surface area $>25\text{ m}^2$, maximum of 22 min). For bottle trapping, plastic funnel traps were made from 2-L soft drink bottles (Richter 1995; Lauck 2004) and perforated to allow water ventilation. The total amount of bottle traps deployed was relative to the surface area of a wetland (two traps minimum, plus one additional trap per doubling of surface area $>25\text{ m}^2$, maximum of 12 traps). Bottle traps were set after electro-fishing and left in wetlands overnight. Sampling protocol for bottle traps followed Hamer and Parris (2011). Traps were placed into ponds between 20:00 and 00:30 h (GMT +2), and retrieved the following morning. Traps were set for one night at each pond per survey due to time limitations within a sampling season.

Dip-netting was performed using a square framed dip net ($300\times 300\text{ mm}$, 2.5 mm mesh) following trap retrieval in the mornings. The total amount of time spent dip-netting was the same as for electro-fishing. Due to the irregular distribution of larval amphibians in wetlands (Shaffer et al. 1994), traps and dip-net sweeps were scattered proportionally and randomly among micro-habitat types. Sampling protocol for dip-netting followed Hamer and Parris (2011). A binomial key was used to identify amphibian larvae species (Du Preez and Carruthers 2009) and fish species (Skelton 2001).

Micro-habitat variables

Seven variables were used to measure micro-habitat for each wetland: wetland surface area (measured at the high-water mark using a meter-wheel for smaller ponds and ArcGIS 10.0 for large dams); bank slope (water depth measured 1 m from the water edge; conductivity ($\mu\text{S}/\text{cm}^3$); pH; vegetation index (total percentage of the pond covered by aquatic vegetation = emergent + submerged + floating vegetation); shade index; and presence of predatory fish. Emergent and submerged vegetation were defined as vegetation extending above and below the water surface respectively. If 50 % of the pond was covered by emergent vegetation, 70 % by submerged vegetation and 30 % by floating vegetation, index values of 0.5, 0.7 and 0.3 were given respectively and the mean were then calculated from these values. Shade index was calculated by using a digital clinometer to measure the angle between the surveyor at eye-level and the highest peak at the horizon, facing north, east, and west, taking an average value of the three readings, whether the highest structure be a tree, building or hill. Pond water conductivity and pH were measured in 500-mL water samples collected ≈ 1 m from the edge of the water at a depth of 50–100 mm using a handheld electronic multi-meter (YSI 556 MPS). There is usually an increase in conductivity in urban waterways, likely caused by contaminants washed in from roads and other impervious surfaces via surface runoff (Paul and Meyer 2001). We calculated the mean number of predatory fish at each pond using the numbers caught in all detection methods. All survey and variable measurement techniques were performed by one person (DJDK) to eliminate surveyor bias. Predatory fish were defined as those species that are known to prey on frog eggs or tadpoles (Pilliod et al. 2012; K. McHugh, pers. comm.). Although several cyprinid species were detected, they were not included as predatory fish because of the uncertainty and inconsistency of data on the effects of these species on amphibian populations (Pilliod et al. 2012).

Landscape variables

A set of landscape variables were categorized and calculated as measures of urbanization using the ArcGIS 10.0 software package. Earlier studies on the effects of urbanization on amphibians have used the proportion of the landscape surrounding wetlands covered by urban land as a metric of urbanization (Houlahan and Findlay 2003; Gagné and Fahrig 2007; Hamer and Parris 2011). Buffers of 250 m were constructed around each wetland (at the location of sampling) and landscape features were categorized and digitized within each of the 68 buffers. Land surface area was divided into 12 categories from aerial imagery (SPOT 2010; 1:5 000 map resolution), namely agricultural lands, natural veld, impervious surfaces, industrial area, railway, roads, rural settlements, urban central business district (CBD), urban recreational grass or fields, residential area, water surface area, and planted woody patches. The “calculate area” tool was used to obtain the surface area covered by the categories for each wetland’s buffer. Buffer zones of 250 m were used because of the relatively small size of Potchefstroom. Using larger buffer zones would possibly have resulted in homogenizing landscape variables. Furthermore, distances from each site to the CBD and average distances to other ponds were calculated using “distance to point” and “average distance between points” tools respectively in ArcMap.

Ordination and statistical analysis

A biplot diagram was created of the canonical correspondence analysis (CCA) for the number of amphibian larvae according to seven micro-habitat and seven landscape explanatory variables that were recorded for 45 wetlands (seven wetlands were excluded from the analysis due to drought; a further 16 wetlands were excluded due to the absence of frogs from the

ponds). CCA is a direct gradient ordination analysis that produces ordination axes confined to linear groupings of environmental variables (Ter Braak 2000). Arrows at the end of each ordination axis point in the direction of the environmental gradient as identified by the explanatory variables. The longer the arrows in each ordination axis, the stronger correlated explanatory variables are with the ordination axes than those with short arrows. In order to comply with a general rule of thumb to have one variable for every ten samples (Harrell 2001; Wintle et al. 2004) some landscapes were merged to represent broader categories in order to obtain seven useable variables: altitude, green open space (GreenSpace, m², represented agricultural lands, natural grasslands, and urban recreational grass or fields), roads (m²), urban CBD (UrbCBD, m², represented CBD and industrial area), residential area (UrbRes, m², represented high-income residential area as well as rural residential settlements), distance to CBD (CBD_Dist, m), average distance between ponds (PondDist, m). Surfaces categorized as railway, impervious surfaces and woody patches were omitted from the analysis. Species data were presented by the total number of individuals of each species over the four survey periods for the common river frog (*Amietia queckettii*, *Aq*), guttural toad (*Amietophrynus gutturalis*, *Ag*), raucous toad (*A. rangeri*, *Ar*), common caco (*Cacosternum boettgeri*, *Cb*), bubbling kassina (*Kassina senegalensis*, *Ks*), striped stream frog (*Strongylopus fasciatus*, *Sf*), and common platanna (*Xenopus laevis*, *Xl*). Species richness (Sp_Rich) was also included to make an inference on general species diversity from the landscape variables. All ordination analyses were performed using CANOCO 4.5. Transformations included a log₁₀-transformation for pond area, embankment slope, conductivity, pond shading, aquatic vegetation, altitude, distance between ponds and CBD, average distance to other ponds and urban residential area. A log₁₀(x+1)-transformation was calculated for roads area, green open space area, and urban CBD area.

Bayesian analysis

The effects of six micro-habitat variables and four landscape variables on species richness (i.e., number of larval frog species detected at a pond) were assessed using Bayesian inference. The six micro-habitat variables and four landscape variables were incorporated into ten Poisson regression models in a variety of combinations, and included: pond area, pH, slope of embankment, conductivity, aquatic vegetation, predatory fish, area of roads, area of green open space, area of urban CBD, and average distance between ponds. We used uninformative priors for model intercept terms ($a \sim \text{dnorm}[0, 1.0 \times 10^{-6}]$) and the regression coefficients ($\text{beta}[j] \sim \text{dnorm}[0, 1.0 \times 10^{-6}]$, where j is an explanatory variable) in OpenBUGS (Lunn et al. 2000; Spiegelhalter et al. 2007). Explanatory variables were examined for collinearity using Spearman rank correlations and consequently highly correlated variables ($|\rho| \geq 0.4$) were not included into the same model (Online Resource: Table A3). One null model ('no effect') was also included (constant only), resulting in a total of 11 models.

OpenBUGS was used to produce 100 000 samples from the posterior distribution of 11 models after discarding an initial "burn-in" of 10 000 samples. Three Monte Carlo Markov chains were run for each model with a suitable number of iterations so that convergence was reached for all variables on the basis of the Brooks-Gelman-Rubin statistic (i.e., $R < 1.05$). We obtained 95 % Bayesian credible intervals from the 2.5th and 97.5th percentiles of the distribution. Relative fit of the models against model complexity were evaluated using the Deviance Information Criterion (DIC; Spiegelhalter et al. 2002). The best fit of the models were considered to be those with a $\Delta\text{DIC} \leq 2$ ($\Delta\text{DIC} = \text{DIC} - \text{DIC}_{\min}$), although any model with $\Delta\text{DIC} < 10$ was also considered as being potentially relevant (Spiegelhalter et al. 2007; Anderson 2008).

Estimating effect sizes in ecology has the advantage of facilitating comparison of credible intervals with values that are ecologically meaningful, rather than focusing on statistical

significance (McCarthy 2007). We therefore assessed the relative importance of the ten explanatory variables by calculating the multiplicative effect (with 95 % credible interval) of each variable on species richness across the range of the variable. In Poisson regression, the multiplicative effect is calculated as the exponent of the standardized coefficient:

$$E_i = \exp(b_i \times \text{range}_i)$$

where E_i is the multiplicative effect of variable i , b_i is the regression coefficient of variable i , and range_i is the range of values for variable i . A multiplicative effect size of 1 corresponds to no change in species richness, and so an explanatory variable with E_i substantially different than 1 is likely to have a biologically important effect on species richness. Multiplicative effect sizes >1 indicate a positive effect of the explanatory variable on species richness; effect sizes <1 indicate negative effects.

Results

Species distribution

Anuran larvae of eight species were detected during the field surveys (Table 1). *Amietia queckettii* was the most frequently detected species, occurring in 39.2 % of the 61 wetlands (seven sites were excluded because of drought conditions), whereas the *K. senegalensis* was detected in only one pond. The remaining six species were detected in between 6.6 and 26.2 % of the sites (Table 1). The mean number of species per wetland was 1.2 (± 1.07 SD), ranging from 0 to 4. Forty five (73.8 %) wetlands were occupied by at least one species. Species'

Table 1 Larval frog species and predatory fish detected during the study and the number of wetlands (out of 61) where they occurred

Family / Species	Common name	No. of ponds
Anurans Pyxicephalidae		
<i>Amietia queckettii</i>	Common River Frog	24
<i>Cacosternum boettgeri</i>	Common Caco	5
<i>Strongylopus fasciatus</i>	Striped Stream Frog	4
Bufonidae		
<i>Amietophrynus gutturalis</i>	Guttural Toad	16
<i>Amietophrynus rangeri</i>	Raucous Toad	12
Hyperolidae		
<i>Kassina senegalensis</i>	Bubbling Kassina	1
Pipidae		
<i>Xenopus laevis</i>	Common Platanna	16
Predatory fish		
Clariidae		
<i>Clarias gariepinus</i>	Sharptoothed Catfish	2
Poeciliidae		
<i>Gambusia affinis</i>	Mosquitofish	27
Centrarchidae		
<i>Micropterus salmoides</i>	Largemouth Bass	12
Cichlidae		
<i>Tilapia sparrmanii</i>	Banded Tilapia	26

distributions that overlapped the study area but were not detected during the surveys included Power's toad (*Amietophrynus poweri*), the giant bullfrog (*Pyxicephalus adspersus*), the red toad (*Schismaderma carens*), and the tremelo sand frog (*Tomopterna cryptotis*). Although both ephemeral and permanent wetlands were included in the study, drought caused all seven ephemeral ponds to have no water during the four survey seasons and therefore surveys were not conducted at these dry sites. Predatory fish namely sharp-toothed catfish (*Clarias gariepinus*), mosquitofish (*Gambusia affinis*), largemouth bass (*Micropterus salmoides*) and banded tilapia (*Tilapia sparrmanii*) were detected in 64 % of the wetlands (in 2, 27, 12, 26 wetlands respectively), with *G. affinis* and *T. sparrmanii* occurring most frequently (Table 1).

There were no species in ponds in or near the central business district, whereas wetlands occurring on the urban fringe had higher species richness and were dominated by *Amietia queckettii*, *Amietophrynus gutturalis*, *A. rangeri* and *X. laevis* (Fig. 1). *Amietophrynus gutturalis*, *A. rangeri* and *X. laevis* were detected in more ponds inside the urbanized border than outside (Fig. 1, Ag, Ar, XI), whereas *S. fasciatus* was detected in one of the wetlands in the urbanized border and the remaining three populations fell outside of it (Fig. 1, Sf). *C. boettgeri* and *K. senegalensis* were only detected outside of the urbanized area (Fig. 1, Cb, Ks), and *A. queckettii* was detected in an almost equal number of sites outside and inside of the urbanized border (Fig. 1, Aq).

Urbanization and community composition

The first CCA axis for landscape variables (Fig. 2; axis 1) explained 22.9 % of the variability in the species data and 58.0 % of the variability in the species-environment relationship (eigenvalue = 0.721). Axis 1 described a landscape gradient from low altitudes, less roads and green open space, larger residential surface areas with closer average distances between wetlands that are located closer to the CBD (negative values), to higher altitudes with higher surface areas of roads and green open space with wetlands that are spaced further away from one another and also located further away from the CBD (positive values; Fig. 2). Only two species were associated with negative axis 1 scores (*Amietophrynus gutturalis* and *A. rangeri*). *Amietia queckettii* was weakly associated with the positive axis 1 scores, whereas *Xenopus laevis*, *Strongylopus fasciatus*, *Cacosternum boettgeri* and *Kassina senegalensis* had a greater affinity with ponds located at higher altitudes further away from the CBD that had a lot of green open space. Species richness was associated with green open space as well as ponds that have a higher average distance between them.

The second CCA axis (Fig. 2; axis 2) explained 9.8 and 24.9 % of the variability in the species data and species-environment relationships, respectively (eigenvalue = 0.721). Axis 2 described a gradient from higher altitudes and residential surface areas, which are located further away from the CBD but low surface areas of green open space (negative scores), to low residential surface areas as well as high CBD, roads and green open space surface areas located at lower altitudes closer to the CBD (positive scores). *Xenopus laevis* was associated with negative axis 2 scores, whereas *S. fasciatus*, *K. senegalensis* and *C. boettgeri* were slightly associated with positive axis 2 scores. *Amietia queckettii* and *A. rangeri* had a high affinity for high CBD surface areas associated with green open space. Species richness was also associated with positive values of axis 2.

The first CCA axis for micro-habitat variables (Fig. 3; axis 1) explained 20.3 % of the variability in the species data and 66.6 % of the variability in the species-environment relationship (eigenvalue = 0.640). Axis 1 described a gradient from shaded, small and well-vegetated ponds with steep embankment slopes, high conductivity and lower pH levels hosting large number of predatory fish (negative values), to sunny habitats with large pond areas and

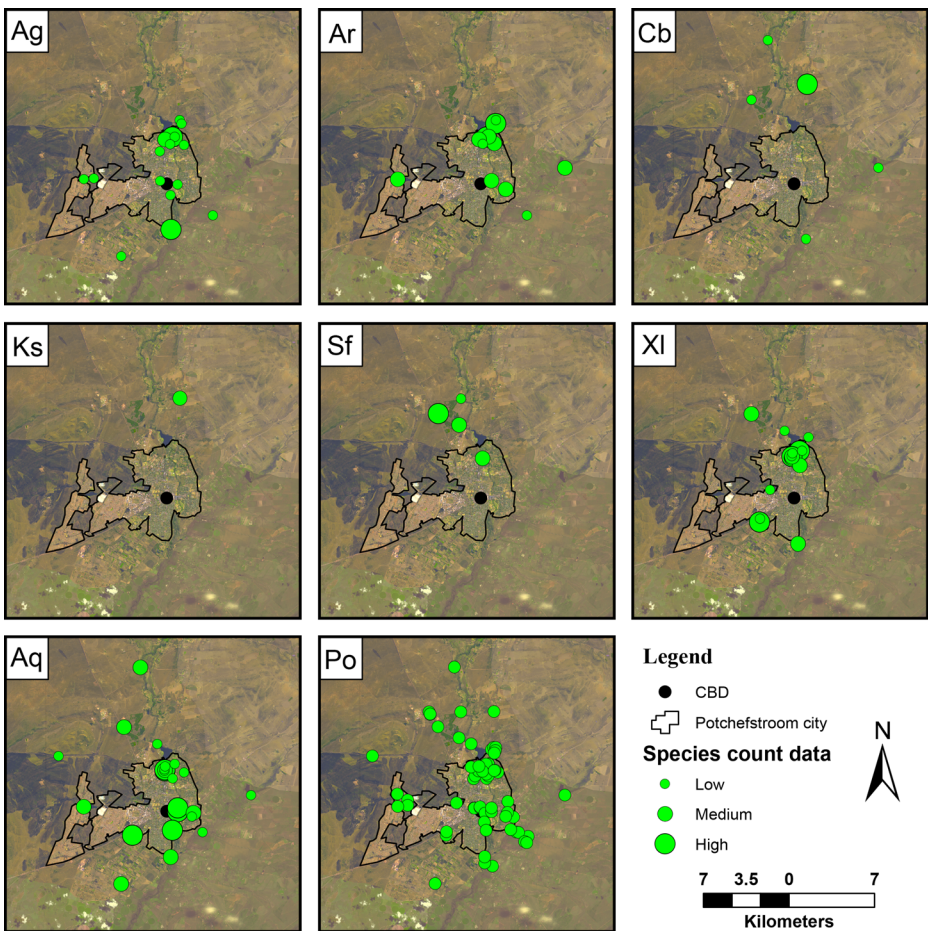


Fig. 1 Distribution maps of each of the seven anuran species detected over a four-season survey. Green circles are representative of the relative count data of each pond for *Amietophrynus gutturalis* (Ag), *A. rangeri* (Ar), *Cacosternum boettgeri* (Cb), *Kassina senegalensis* (Ks), *Strongylopus fasciatus* (Sf), *Xenopus laevis* (XI) and *Amietia quecketti* (Aq). Green circles in last map (Po) show the locations of each of the surveyed ponds in order to compare the presence of the species distribution. Potchefstroom area excludes agricultural landscape. Black patches on the aerial image show areas of field that were burned due to accidental fires or firebreaks

gentle slopes having less vegetation and a low number of predatory fish, low conductivity and higher pH levels (positive values; Fig. 3). *Cacosternum boettgeri*, *K. senegalensis*, and *S. fasciatus* were associated with the positive scores of axis 1, whereas *A. quecketti* and *X. laevis* were slightly associated with negative scores. *Amietophrynus gutturalis* and *A. rangeri* were both grouped in the middle of the CCA-plot where axis 1 and 2 crossed, possibly indicating that they exhibit generalized habitat preferences, and species richness was not associated with either positive or negative values in axis 1. The second CCA axis (Fig. 3; axis 2) explained 6.3 and 20.7% of the variability in the species data and species–environment relationships, respectively. *C. boettgeri* and *K. senegalensis* were associated with ponds with limited vegetation, steep bank slopes and larger pond areas with lower conductivity and pH levels (Fig. 3), whereas *A. quecketti*, *X. laevis* and *S. fasciatus* were more associated with these conditions.

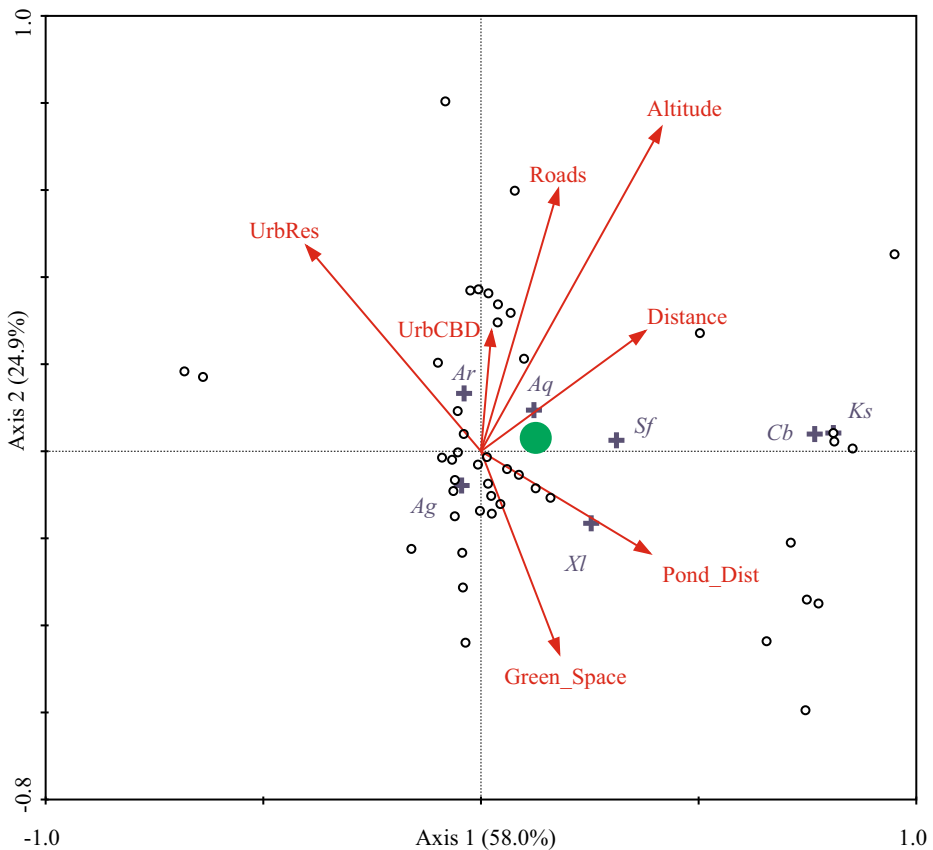


Fig. 2 Ordination diagram (biplot) of the canonical correspondence analysis (CCA) for the number of amphibian larvae according to seven landscape explanatory variables recorded at 45 wetlands in Potchefstroom, South Africa, 2012–2013. Species are presented as blue crosses; sample sites are presented as open circles; number of species (species richness) occurring at a wetland is presented as a solid green circle. Species codes according to Fig. 1

Three models that predicted species richness of the frog breeding assemblages were identified based on DIC values ($\Delta\text{DIC} < 2$) as having better relative fit than the remaining eight models (models 4, 9 and 10; Table 2). Model 4 included local habitat variables vegetation, predatory fish and pond area (see Table 3 for regression coefficients). Vegetation was the only variable in model 9 (together with the constant). In terms of supported models, model 10 included a landscape variable (surface area of urban CBD) and each model included vegetation. In the remaining eight models, there was lowest support for the models in which landscape variables dominated (model 6; $\Delta\text{DIC} = 7.4$) and for the null model there was also low support (constant only; model 1; $\Delta\text{DIC} = 5.1$).

Local habitat variables had larger effect sizes (Fig. 4a–f) than the comparatively weaker evidence for an effect of landscape variables on species richness (Fig. 4g–i; also see Table 2). Multiplicative effects of surface area covered by roads and green open space were small (i.e., values at or close to 1); there was a small positive effect of green open space on species richness and a small negative effect of roads (Fig. 4g and h). There was stronger evidence of a negative effect of urban CBD on species richness, with an average multiplicative effect size of 0.46 across

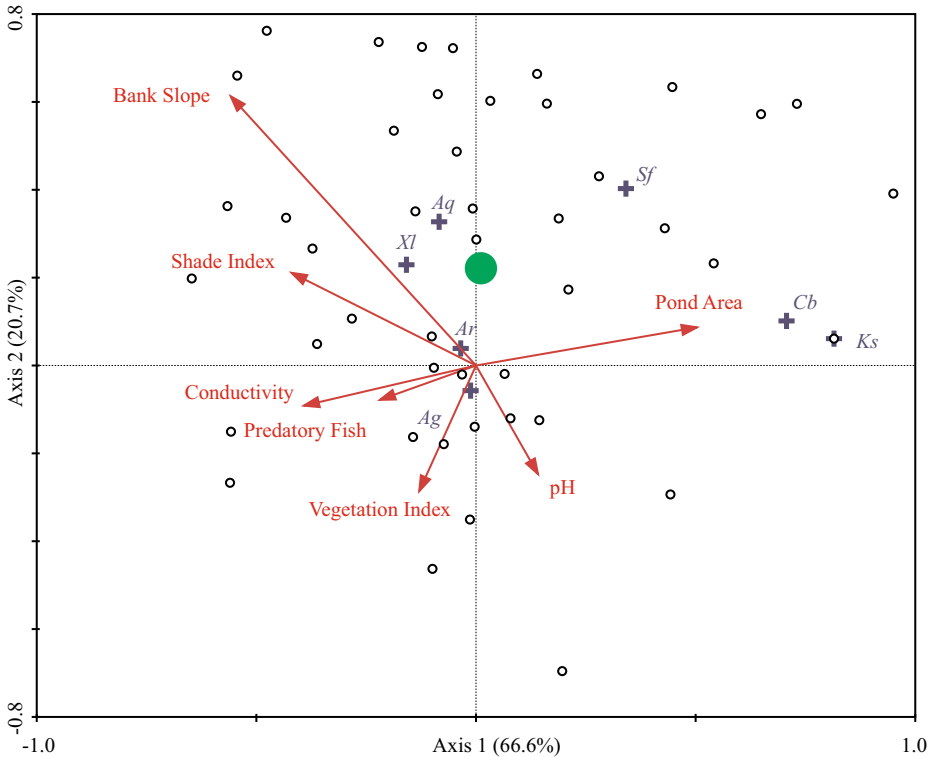


Fig. 3 Ordination diagram (biplot) of the canonical correspondence analysis (CCA) for the number of amphibian larvae according to seven micro-habitat explanatory variables recorded at 45 wetlands in Potchefstroom, South Africa, 2012–2013. Species are presented as blue crosses; sample sites are presented as open circles; number of species occurring at a wetland is presented as a solid green circle. Species codes according to Fig. 1

the four models that included this variable (Fig. 4i). This translates to the prediction that, holding all other variables constant, a pond surrounded by the highest proportion of urban CBD within 250 m radius (i.e., 5.1 ha) would have 42–51 % of the species detected at a pond with no surrounding urban CBD. There was no or only minor overlap of the 95 % credible intervals with one for the means of the four models, indicating an acceptable level of certainty in the estimates.

At the local scale, there was strong evidence of a positive effect of aquatic vegetation on species richness, with an average multiplicative effect size of 2.7 for models 2–5 and 8–10, and with most 95 % credible intervals not encompassing one (Fig. 4d). This translates to the prediction that, when all other variables are held constant, we can be certain that a pond containing the highest proportion of aquatic vegetation would have 2.4–3.1 times the number of species detected at a pond with no vegetation.

Discussion

Species-specific responses to habitat variables

We found many species-specific responses to urbanization and that our study agrees with others conducted in urban landscapes in that it stresses the importance of terrestrial habitat and

Table 2 Deviance information criterion (DIC) values for the 11 Poisson regression models of species richness at a pond. Best fit models are presented in bold with Δ DIC <2

Model	Variables	DIC	Δ DIC†
1	constant	175.2	5.1
2	constant, area, slope, conductivity, vegetation, fish	172.6	2.5
3	constant, slope, conductivity, vegetation, shade, fish	173.8	3.7
4	constant, area, vegetation, fish	170.6	0.5
5	constant, area, pH, slope, conductivity, vegetation, fish	174.5	4.4
6	constant, roads, green, urbCBD	177.5	7.4
7	constant, ponddist	176.4	6.3
8	constant, area, vegetation, fish, roads, green, urbCBD	175.2	5.1
9	constant, vegetation	170.6	0.5
10	constant, vegetation, urbCBD	170.1	0
11	constant, urbCBD	174.6	4.5

Area, $\log_{10}(\text{area})$; slope, $\log_{10}(\text{slope})$; conductivity, $\log_{10}(\text{conductivity})$; shade, $\log_{10}(\text{shade})$; fish, mean [*Gambusia affinis* + *Clarias gariepinus* + *Micropterus salmoides* + *Tilapia sparrmanii*]; roads, $\log_{10}(\text{area of roads} + 1)$; green, (area of green open space + 1); urbCBD, $\log_{10}(\text{area of urban CBD} + 1)$; ponddist, $\log_{10}(\text{average distance between ponds})$

†Difference in DIC value for a particular model when compared to the top-ranked model (model 10)

aquatic vegetation for amphibians (see Semlitsch 1998; Smith and Green 2005; Pillsbury and Miller 2008; Hamer and Parris 2011; Scheffers and Paszkowski 2013). At a species level, *Amietophrynus spp.* were habitat generalists that were distributed broadly in the urbanized landscape and had no specific affinity for any of the micro-habitat variables. Species vary in their response to changes in the physical environments and therefore adaptability to the changes brought about by urbanization (Adams 1994; Blair 2001). Blair (2001) categorized the reaction of species to human activities in three types, namely ‘urban avoiders’, ‘urban

Table 3 Coefficients of the explanatory variables included in the three best Poisson regression models of species richness (models 4, 9 and 10). Means are presented from the posterior distribution with standard deviation (SD) and 95 % Bayesian credible intervals (2.5 and 97.5 %)

Variable	Mean	SD	2.5 %	97.5 %
Model 4				
Constant	0.15	0.12	-0.09565	0.3857
Area	0.13	0.09	-0.04071	0.305
Vegetation	0.50	0.24	0.0246	0.9625
Fish	0.14	0.09	-0.04617	0.3069
Model 9				
Constant	0.19	0.12	-0.0439	0.4175
Vegetation	0.58	0.22	0.1397	1.005
Model 10				
Constant	0.16	0.12	-0.09444	0.3901
Vegetation	0.59	0.23	0.14	1.043
urbCBD	-0.18	0.12	-0.4318	0.01919

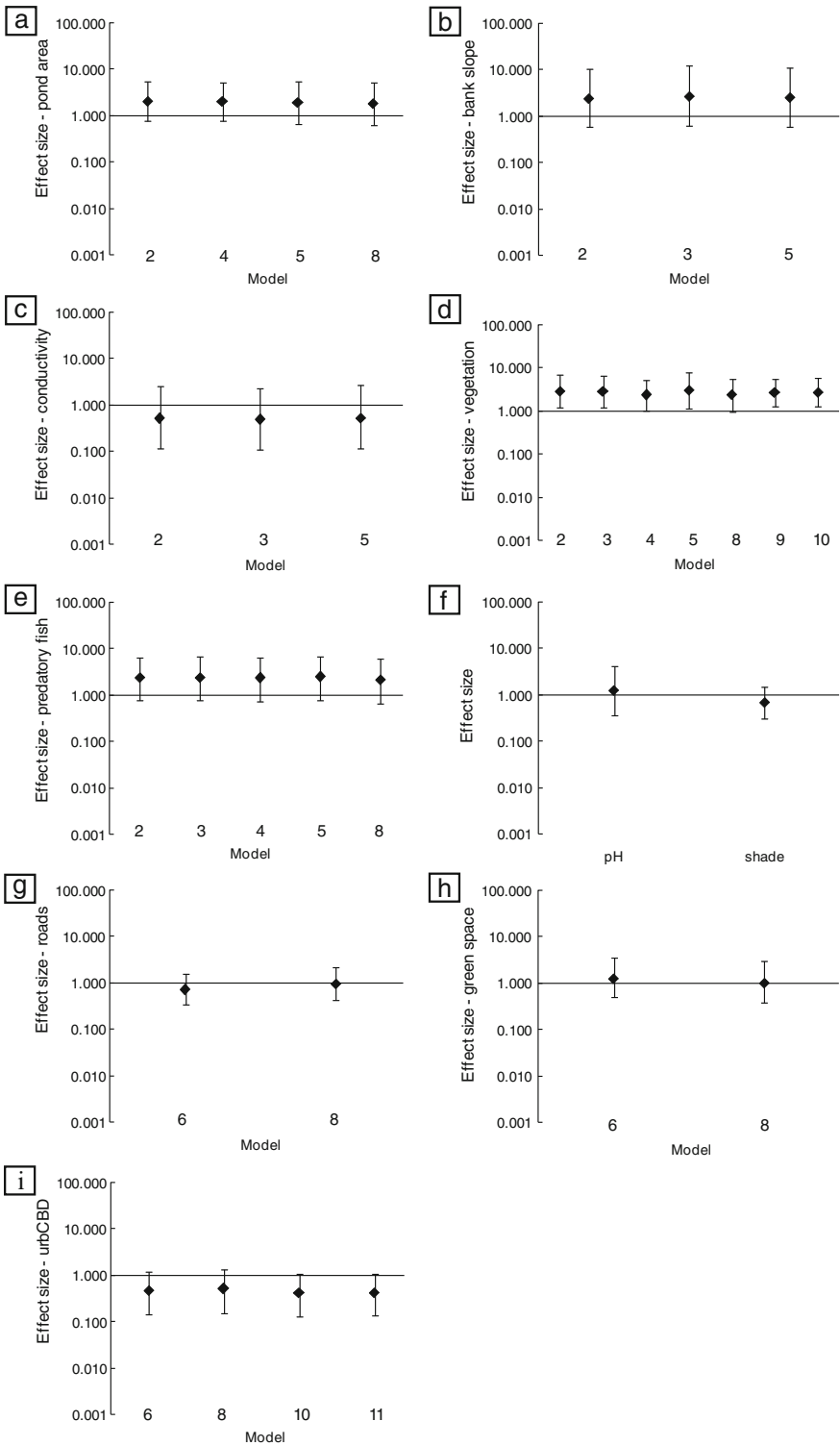
See Table 2 for a description of variables

adapters', and 'urban exploiters'. *Amietophrynus spp.* are comparable to 'urban adapters' because they often use constructed garden ponds for breeding, but are not principally reliant on human resources ('urban exploiters') but also not principally reliant on natural resources ('urban avoiders'). *Amietophrynus* species aggregate in large, loud choruses and females produce long gelatinous strings containing thousands of eggs, which may contribute to their adaptability in urban settings.

Amietia queckettii was detected at more ponds than any other species (39.2 % of the 61 wetlands) within a variety of wetland types. This may be partly explained by the exclusion of competition for habitat availability due to its winter-breeding behaviour (Bonnet et al. 1998; Voituron and Lengagne 2008). This species also utilize streams, rivers and other permanent water bodies such as garden ponds and dams (Channing 2001; Du Preez and Carruthers 2009). *Amietia queckettii* was also grouped with the *Amietophrynus spp.* in terms of micro-habitat, but showed a high affinity for urban landscapes as well as green open space. This species may be able to tolerate the disturbed physical conditions prevalent in the more urbanized areas because of its extended breeding season and broad habitat utilization, as showed in studies of species with similar characteristics (Blaustein 1994; Blaustein and Wake 1995). Due to specific habitat requirements (gradual bank slope, well-vegetated large ponds) and association with ephemeral wetlands, *C. boettgeri* and *K. senegalensis* were not found near developed areas, and therefore are sensitive to urbanization. None of these species occurred within the urbanized landscape and can therefore classify as an 'urban avoider' that are very sensitive to human persecution and habitat disturbances (McKinney 2002). *Strongylopus fasciatus* was associated with large, well-vegetated ponds and could be found in residential areas. *Xenopus laevis* was associated with larger and deeper (i.e., steeper embankment slope) ponds showing an affinity with urbanized landscapes, high wetland connectivity and presence of predatory fish, which is typical of primarily aquatic breeders. Dispersal abilities for most of South African frog species have not been determined and the relatively low dispersal capabilities (vagility) of some species will be affected worse (Sinsch 1990; Gibbs 1998; deMaynadier and Hunter 2000; Bowne and Bowers 2004).

Species richness response to local habitat variables

Our results demonstrated a strong correlation between species richness and aquatic vegetation. Species diversity is known to escalate with an increase in vegetation diversity, primarily due to the increase in habitat heterogeneity (Hazell et al. 2001; Jansen and Healey 2003; Hazell et al. 2004; Lemckert et al. 2006; Lane et al. 2007). Aquatic vegetation provides locations for oviposition for frogs (Egan and Paton 2004) and for predator avoidance by larvae (Tarr and Babbitt 2002). Our results show that higher species richness and an increase in aquatic vegetation were also accompanied by an increase in predatory fish. Studies have demonstrated that the presence of vegetation would create considerable habitat heterogeneity and therefore shelter for tadpoles escaping from fish predators (Hecnar and M'Closkey 1997; Hazell et al. 2001; Tarr and Babbitt 2002; Lane et al. 2007). While the positive relationship between species richness and abundance of predatory fish may seem counterintuitive, it is likely that either other unmeasured habitat variables relate positively to both frogs and fish, or that predation by fish is reducing densities of some abundant species and leading to competitively-inferior species being able to exploit limited resources in a pond, thereby resulting in more species at a pond. Nonetheless, other studies conducted in urban landscapes reported a negative effect of predatory fish on amphibian community assemblages and abundance (Hamer and Parris 2011, 2013).



◀ **Fig. 4** The multiplicative effect of ten explanatory variables (means and 95 % credible intervals) on larval frog species richness predicted by models with Δ DIC <10 for ponds in Potchefstroom, South Africa. Multiplicative effects for pond area were predicted by model 2, 4, 5 and 8 (a); effects for bank slope and conductivity were predicted by models 2, 3 and 5 (b, c); effects for vegetation were predicted by models 2–5 and 8–10 (d); effects for the presence of predatory fish were predicted by models 2–5 and 8 (e); effects for pH and shade were predicted by models 5 and 3 respectively (f); effects for roads and green open space surface area were predicted by models 6 and 8 (g, h); effects for urban CBD surface area were predicted by models 6, 8, 10 and 11 (i). Multiplicative effect sizes >1 indicate a positive effect of the explanatory variable on species richness; effect sizes <1 indicate negative effects

In this study, conductivity and pH showed only weak effects on species richness. Conductivity is known to reduce larval survival and development (Griffis-Kyle and Ritchie 2007; Snodgrass et al. 2008) and negatively impacts anuran species richness and community composition (Hamer and Parris 2011). Urban stormwater run-off may cause increased conductivity levels (Dow and Zampella 2000; Paul and Meyer 2001), but may also be influenced by other factors. For example, one of the study sites (Wasgoedspruit vlei) is downstream of a gypsum mine that may explain abnormally high conductivity levels. No anuran larvae or fish species were detected in this wetland and dead crabs were observed by DJDK.

Species richness response to landscape habitat variables

The best model of species richness (model 10) included vegetation (positive effect) and surface area of urban CBD (negative effect). Urban CBD surface area indicated a moderately strong multiplicative effect size of 0.46. On larger spatial scales than this study, decreases in amphibian species richness have been observed in wetlands surrounded by high human population densities and urban land (Rubbo and Kiesecker 2005; Pillsbury and Miller 2008; Hamer and Parris 2011). Decreases observed in these studies were attributed to landscape fragmentation caused by roads, buildings, and houses that obstruct many frog species as they disperse among corresponding habitats, and disrupts metapopulation dynamics (Gibbs 1998; Parris 2006). However, the remaining landscape variables (namely, roads surface area, green open space surface area and average distance to ponds) only indicated weak effects, and inferences on these statistics should be made with great care.

The very weak support demonstrated by the model including purely landscape variables (Δ DIC=7.4) contradicts previous studies on anuran assemblages along urban–rural gradients (Pillsbury and Miller 2008; Hamer and Parris 2011; Scheffers and Paszkowski 2013). The unsupported models do not imply that landscape variables do not play a role in habitat determinants; rather we propose that it is due to the small size of Potchefstroom as a city, lacking the road density of larger cities (e.g., Melbourne, Australia; Hamer and Parris 2011). Ponds surrounded by large areas of green open spaces may have greater habitat connectivity with surrounding ponds and wetlands, thereby assisting in dispersal and may also provide habitat to forage and hibernate (Hamer and Parris 2011). The Mooi River bisects Potchefstroom, providing a green open area strip on both sides of the river. Green open space running along rivers provides dispersal corridors for both fauna and flora (Good 1998; Säumel and Kowarik 2010).

Management and conservation implications

Overall, species richness was associated with well-vegetated wetlands, low urban CBD surface area and conductivity, large pond areas and steeper bank slopes. Habitat generalist species bias the distribution towards the urban fringe of the town and species showing habitat specificity

occurred in areas of low habitat alteration due to urbanization. These results underscore the importance of habitat heterogeneity (e.g., aquatic vegetation) within wetlands and shows that the effects of urbanization in smaller developing towns shape the amphibian community structure even at early stages of infrastructure development. Although our study in Potchefstroom demonstrated that a number of habitat generalist anuran species are still persisting close to the CBD, it may only be a matter of time before these local populations go extinct due to their isolation by urban infrastructure, and as such cannot be easily recolonized by individuals following local extinction (Semlitsch 2000). For example, time lags in the response of amphibian communities to residential development have been reported elsewhere (Gagné and Fahrig 2010). Although restricted to the Potchefstroom area, the response of the community structure of anurans to an urbanization gradient was the first reported for a South African city and concurs with studies on the effects of land use on anuran species composition in southern Africa (Russell and Downs 2012; Trimble and Van Aarde 2014). To cater for the ecological requirements of the amphibian community in Potchefstroom, and potentially other rapidly-developing African cities, we recommend planting and maintaining endemic aquatic vegetation in ponds and wetlands, and ensuring habitat connectivity among both terrestrial and aquatic habitats. With the correct resource management and urban design of the fast development of Potchefstroom, the Mooi River may provide a key area for habitat connectivity, not only for anurans, but other riverine dependent fauna and flora as well (Good 1998; Säumel and Kowarik 2010; Hamer and Parris 2011).

In conclusion, this study gives emphasis to the value of a multi-spatial approach to amphibian conservation in urban and urbanizing areas. Although the drought condition biased the ponds towards permanent wetlands and consequently inferences on hydroperiod were a limitation, this study highlights the species specific responses to urbanization as observed within an urban and urbanizing landscape. This study will serve as a foundation for future studies on the response of African amphibians to urbanization.

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