

Research paper

Waterbird community composition, abundance, and diversity along an urban gradient

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ABSTRACT

Urban riparian corridors have the capacity to maintain high levels of bird abundance and biodiversity. How riparian corridors in cities are used by waterbirds has received relatively little focus in urban bird studies. The principal objective of our study was to determine how habitat and landscape elements affect waterbird biodiversity in an arid city. We surveyed 36 transects stratified across a gradient of urbanization and water availability along the Salt River, a riparian corridor that is monitored as part of the Central Arizona-Phoenix Long-Term Ecological Research study system located in Phoenix, Arizona, USA. Habitat and landscape variables were reduced via Principal Component Analysis to be used in a constrained ordination that identified waterbird community composition patterns, and then used to model the responses of guild abundance and diversity. Habitat and landscape components from the constrained ordination explained 39% of the variation in the waterbird community. Land use components were related to the suite of species at each site, but had a weaker relationship to guild abundance or diversity. Habitat-level components (water physiognomy, shoreline composition, and terrestrial vegetation cover) were more important in predicting both guild abundance and diversity. We found that water physiognomy was the strongest driver shaping waterbird community parameters. The implications of our study are relevant to urban planning in arid cities, offering the opportunity to design and improve wildlife habitat while providing other important public amenities.

1. Introduction

Globally, urban land area increased by 58,000 km² between 1970 and 2000 (Seto, Fragkias, Güneralp, & Reilly, 2011). Cities continue to expand outward, urban and exurban settlement covers four to five times the area it did in 1950 (Brown, Johnson, Loveland, & Theobald, 2005) and urban land area is expected to triple by 2030 (Seto, Güneralp, & Hutrya, 2012). Twenty-nine of the world's ecoregions, which house 3056 species and 213 endemic species, have at least a third of their total area urbanized (McDonald, Kareiva, & Forman, 2008). Rapidly expanding urban areas necessitate a better understanding of how biodiversity in urban environments is influenced by human decisions that affect habitat characteristics (Hostetler and Knowles-Yanez, 2003).

Urban research has highlighted key biodiversity trends that span numerous taxa and geographical locations. Generally, cities have a higher abundance of commensal and generalist species, but lower biological diversity than non-urban landscapes (McKinney, 2008). In dense urban areas, bird abundance is often high and richness is low, whereas avian richness often peaks in areas of intermediate urban

density (e.g., Blair, 1996; Melles, Glenn, & Martin, 2003). Land use, available habitat, and socioeconomic factors can all affect biodiversity patterns within the urban matrix (Melles, 2005; Lerman & Warren, 2011). The numerous studies of urban bird biodiversity often focus on terrestrial species, but there has been less focus on how waterbirds respond to urbanization. Waterbird communities may respond differently to urbanization than terrestrial species because of their unique habitat and foraging requirements.

Waterbirds are a diverse group of species closely associated with freshwater and marine habitats, and are important as both indicators of ecosystem health (Ogden et al., 2014) and as a source of recreational revenue (Carver, 2009). Regardless of their importance, global waterbird populations are declining (Wetlands International, 2012). One main cause of the decline is the increase in anthropogenic land-uses, reducing habitat availability at stopover and wintering sites (Page & Gill, 1994). In arid regions, water is a highly variable resource and aquatic habitat is especially important for waterbirds, making habitat loss an important issue (Kingsford, Roshier, & Porter, 2010). Despite their limited extent, mesic strips of riparian habitat in desert regions

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stand in a stark contrast to an otherwise arid landscape, providing wintering and stopover sites (Patten, 1998; Flannery et al., 2004; Villaseñor-Gómez, 2008). Urbanization reduces or modifies aquatic habitats for waterbirds by diverting water for municipal purposes, creating habitat from built infrastructure, or modifying existing streams, floodplains, and wetlands (Grimm, Faeth, Golubiewski, Redman, Wu, & Briggs, 2008). However, in arid regions, the loss of existing aquatic and semi-aquatic habitat due to development can be paralleled by a net increase in overall water availability through built habitat such as artificial lakes or constructed wetlands (Larson & Grimm, 2012).

Findings from Rosa et al. (2003) suggest that waterbird species richness in arid environments decreases only when disturbance encroaches on the wetland, narrowing the width or changing the structure. Another urban study in the non-arid state of Florida found that waterbird guilds have a significantly higher than expected richness along developed shorelines compared to undeveloped habitat (Traut & Hostetler, 2004). In this study, our goal is to further investigate if waterbirds take advantage of non-traditional aquatic habitat along an urban riparian corridor and, if so, what biophysical features of the habitat are most important in supporting a diverse community. Specifically, our research objectives are to: (1) identify how waterbird diversity shifts along a gradient of urbanization and water availability, and (2) determine the relationship between habitat and landscape elements with waterbird community parameters (guild abundance, community composition, and diversity).

2. Methods

2.1. Study area

The Phoenix Metropolitan Area is one of the fastest growing cities in the United States, with an estimated population of over 4.4 million as of April 2014 and a growth rate of 4% per year in the last 40 years (US Census, 2015). The Salt River is a river that is diverted by the Granite Reef Diversion Dam into canals as part of the Salt River Project to provide drinking and irrigation water to Phoenix. The majority of the riverbed that passes through Phoenix is dry, with the exceptions of patchy ephemeral and perennial water sources. The result is a highly heterogeneous riparian corridor with patchy habitat characteristics spread throughout the extent of the river. The surrounding matrix is equally variable, comprising desert, urban, and agricultural land use and cover. Our study focused on a 75-kilometer segment of the Salt River that spans the Phoenix metropolitan area (Fig. 1), starting at Saguaro Lake (33.5656, -111.5361) and ending at the Gila River confluence (33.3811, -112.3131).

2.2. Avifauna

The waterbird community was surveyed during the winters of 2015 and 2016 (December–February) at 18 transects 225 m in length per winter, for a total of $n = 36$ transects (Fig. 1). Transects were randomly placed parallel to the water's edge, stratified along gradients of water availability (dry, ephemeral, perennial) and level of urbanization (urban, intermediate, and desert). The sampling scheme resulted in transects that were at least 700 m apart, which meets the recommendations that transects be at least 200 m apart in dense environments and at least 500 m apart in open environments to produce independent samples and reduce spatial autocorrelation for bird studies (Sutherland, 2006). Surveys were conducted in the winter when most waterbirds migrate through the region. We used the line transect method (Bibby, Burgess, Hill & Mustoe, 2000) to conduct community surveys, recording waterbirds within 150 m of the transect center (sensu DeLuca, Studds, King, & Marra, 2008; Rathod & Padate, 2007; Roy, Goswami, Aich, & Mukhopadhyay, 2011). Trained observers slowly walked along the edge of the stream bed to flush cryptic or

hidden species and recorded any birds seen or heard within the truncation distance. Counts occurred within 4 h of sunrise, with wind below 20 km per hour and precipitation no heavier than a light drizzle. Surveys were completed three times per winter season (Conway, 2011). On repeat visits, the site order and direction that the observer walked (up or downstream) were rotated to reduce bias.

Community measurements of guild abundance and diversity were derived from bird surveys pooled over two years of sampling because there was no significant difference in guild abundance or richness between the two years, and year-effects were not the focus of our study. Birds were classified into six guilds (dabbling ducks, diving ducks, fish-eating birds, rails, shorebirds, and wading birds) primarily based on bird foraging strategies and functional traits (Elphick & Dunning, 2001; Appendix I). Prior to analysis, species abundance for each site was standardized by the area of water so that abundance data were interpreted as usage per available habitat, or the relative abundance. Guild abundance was calculated as the sum of total individuals per guild averaged over the three visits and log-transformed to normalize the data. We calculated species richness by summing total species detected on any one the surveys at each transect. We determined waterbird diversity by calculating the Shannon Diversity Index at each site (Hill, 1973).

We visualized the Renyi diversity profiles of sites grouped according to their position within level of urbanization and water availability (Hill, 1973). The Renyi diversity profile shows biodiversity across multiple indices. The horizontal axis (H-alpha) represents a range of indices that emphasize richness and evenness (low x-axis values) to those that emphasize abundance (high x-axis values). The 12 sites with highest levels of urbanization were assigned to 'urban', followed by the next 12 being placed into 'intermediate' and the final 12 with the lowest levels of urbanization along the gradient were considered 'desert'. This was repeated for the four levels of water availability.

2.3. Land cover classification of study area

We performed a supervised land cover classification with ERDAS Image software (2006) based on the Landsat 8 Satellite imagery (11 bands and a 30 m resolution), acquired in February 2015. In supervised classification the analyst selects representative samples for each land cover class, known as 'training sites.' The spectral signatures of training sites are then used to determine the land cover class for each raster cell by pattern matching using maximum-likelihood classification. The land cover classification included seven categories: urban/developed (residential, industrial, and commercial land use), cultivated vegetation (agriculture, irrigated grass, golf courses, and mesic yards), riparian vegetation, impervious surface, water, river gravel, and undeveloped (desert, desert shrub, urban desert remnant parks). The supervised classification results were confirmed in the field at the sampling locations. The land cover classes were then reclassified into separate rasters in order to derive habitat and landscape variables. The water classification raster was converted to polygons and combined with a shapefile mapping artificial lakes in Phoenix (Larson & Grimm, 2012) to ensure that all water was mapped as accurately as possible and to capture any cells that may have been misclassified in the supervised classification.

2.4. Environmental variables

For each transect, we quantified 20 environmental variables categorized as habitat or landscape scale (Table 1). Variable measurements were made from the land cover classification or directly from the Landsat 8 satellite data. Analyses were performed in ArcMap 10.1 geographic information system (ESRI 2006) and measurements were verified in the field for each transect.

We used the land cover classification and unclassified imagery to measure 12 habitat variables (Table 1) within 150 m of either side of the transect, encompassing a total area of 225 m × 300 m. Similar to

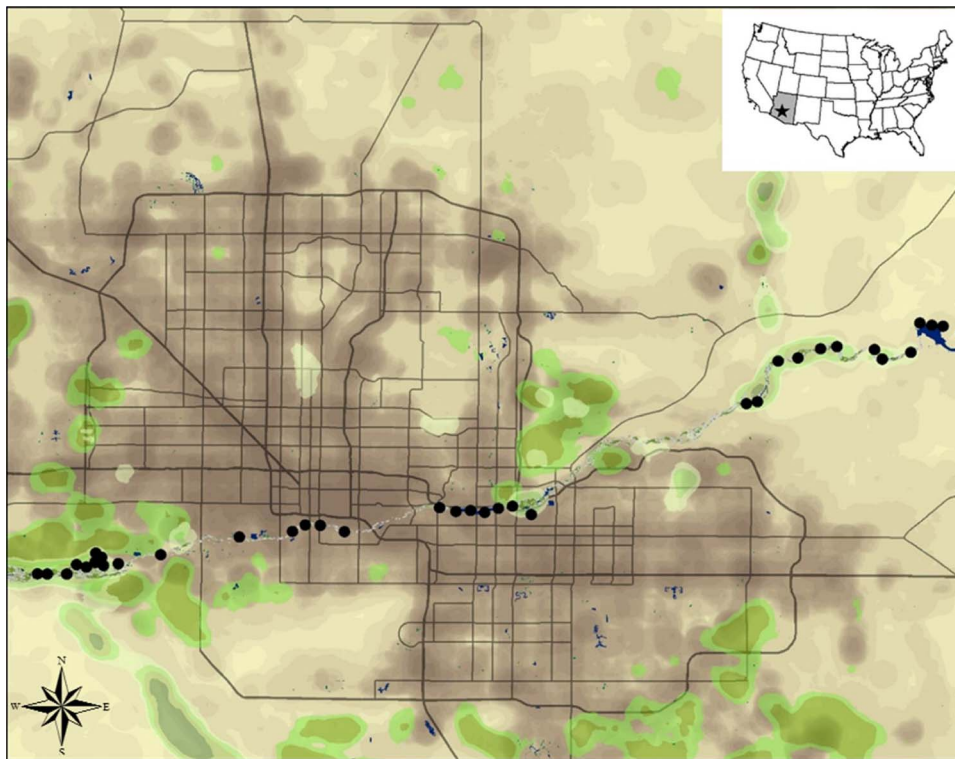


Fig. 1. Location of the study area in Phoenix, Arizona, USA surveyed during the winters (between December and February) of 2014–2016, three times per year. 36 transects (black dots) were randomly stratified along a gradient of water availability and urbanization (desert, urban, and intermediate) at least 700 m apart. Landscape depicted shows an overlay of urbanization (brown to tan), cultivated vegetation (light green), canopy cover (olive green), and water area (blue to grey) based on land cover classification rasters; major roads shown for reference. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Germaine, Rosenstock, Schweinsburg, and Richardson (1998) and Lerman and Warren (2011), we chose a habitat plot width two times that of the bird sampling transect. Canopy cover was measured as the percentage of riparian vegetation per the total area of each transect using the classified raster. We calculated the normalized difference vegetation index, or NDVI, $(NIR - Band\ 4 / NIR + Band\ 4)$ from the unclassified imagery as a measure of greenness (Tucker, 1979) using ArcMap 10.1. Three of the habitat variables were measured using the ‘water’ classification raster converted into a polygon shapefile. Connectivity was defined as the distance (km) to the next closest water polygon. Higher values denote lower levels of connectedness as the distance between water bodies increases. Area and edge ratio were

collected for the water polygons delimiting each body of water. Area was defined as the total area of the water polygon where each transect was located (hectare). The edge ratio describes the shape of the body of water and was defined as the length of perimeter (km) per area of water (hectare). Higher edge ratio describes bodies of water with complex shorelines and maximized perimeter per area of water, smaller values would describe large, round bodies of water. Perching structure was the sole habitat variable derived from direct field observations. Each transect was assigned as a categorical value from 1 to 36, with 1 representing transects with the lowest available amount of perches available. Perching structure included concrete pillars, vertical vegetation, or buoys.

Table 1
Descriptive statistics and sampling methods for 20 habitat and landscape level environmental variables measured at 36 transects located along the Salt River in Phoenix, Arizona, USA between the winters (December-February) of 2015 and 2016.

Environmental Variables	Mean ± SE	Sampling Method
Habitat		
Emergent vegetation (%)	15.89 ± 2.34	% of 100 points that were emergent vegetation
Open water (%)	26.56 ± 3.63	% of 100 points that were open water
Cobblestone (%)	10.61 ± 2.27	% of 100 points that were cobblestone
Extent (ha)	21.90 ± 5.19	Total area of surrounding body of water (hectare)
Connectivity (m)	197.67 ± 33.69	Distance to next closest body of water (m)
Edge ratio (km/ha)	0.43 ± 0.06	Perimeter of shoreline (km) per area water (hectare)
Perching structure	6.81 ± 0.95	Rank index (scale of 36) of perching structure available
Impervious surfaces (%)	12.50 ± 1.77	% of 100 points that were impervious surface
Bare ground (%)	15.00 ± 2.16	% of 100 points that were bare ground or gravel
Canopy cover (%)	15.15 ± 2.37	% of transect with vegetation classification
NDVI (INT)	136.87 ± 1.33	Average NDVI of transect
Tree/shrub (%)	19.44 ± 1.14	% of 100 points that were tree or shrub cover
Landscape		
Distance to desert (km)	3.57 ± 0.66	Distance to closest continuous (> 2000 m ²) desert patch (km)
Cultivated vegetation (%)	12.07 ± 2.0	% agriculture in 1.5 km buffer
Urban development (%)	15.23 ± 2.83	% urban and impervious surface in 1.5 km buffer
Riparian vegetation (%)	24.51 ± 3.37	% vegetation in 1.5 km buffer
Water (%)	6.39 ± 1.24	% Water in 1.5 km buffer
Distance to agriculture (km)	5.33 ± 0.96	Distance to closest agricultural field (km)
Isolation ratio	530.7 ± 149.6	Urban developed to water ratio in 1.5 km buffer
River gravel	10.95 ± 1.25	% of river gravel land cover in 1.5 km buffer

The remaining seven habitat variables were collected using a dot-grid overlay (see Blair, 1996; Melles et al., 2003), on the unclassified Landsat imagery from February 2015. Emergent vegetation, open water, cobblestone, tree/shrub, impervious surface, and bare ground were calculated as percentages for each transect. To calculate percentages, 100 points were randomly placed over the 225 m × 300 m buffer using the ‘Generate Random Points’ tool, then each point was categorized into one of the seven variables.

A total of eight landscape variables were measured using the land cover classification to describe the matrix surrounding the riparian area. We collected two distance measurements: distance to desert (km) and distance to agriculture (km) by measuring the distance from the transect center to the closest habitat patch for each respective land cover class. For the remaining six landscape-level variables, we used a 1.5 km buffer around the center point of each transect to quantify surrounding land use and cover type. Cultivated vegetation, urban development, riparian vegetation, river gravel, and landscape level water were quantified as the percent of cells within each 1.5 km buffer. We defined the isolation ratio for each transect as the ratio of the area of water to the area of urbanization and impervious surface. Higher isolation ratio values describe a large amount of water available across the landscape, smaller values describe smaller water bodies interspersed throughout urban land use.

2.5. Statistical analysis

Prior to analysis, we calculated a Pearson Product-Moment correlation coefficient for each pair of the 20 environmental variables to identify any multicollinearity. As a result, we found that the environmental variables were highly correlated to one another (Supplementary Material Fig. S1). We addressed the problem of multicollinearity in the environmental variables by using a Principal Component Analysis (PCA) to derive a set of uncorrelated, synthetic components. We used two distinct PCAs to separate the habitat and landscape variables into components.

Twelve variables went into the habitat PCA (area, perching, open water, connectivity, cobblestone, emergent vegetation, edge ratio, canopy cover, NDVI, tree/shrub cover, impervious surface and bare ground) and eight variables were used in the landscape PCA (distance to desert, cultivated vegetation, disturbed land use, distance to agriculture, riparian vegetation, water, gravel, and isolation). We scaled and centered the environmental data prior to the PCA. The resulting components that had an eigenvalue summed to > 1 were selected to represent the original variation in the environmental data (Kaiser, 1960). Components were interpreted based on their variable loadings, where variables with the largest scores for each component had a larger weight when defining its characteristics (Legendre & Legendre, 1998). We then used the synthetic components derived from the PCA as independent variables in subsequent analysis to eliminate multicollinearity while retaining the variation of the environmental variables for the models.

To determine how habitat and landscape components affected waterbird community assemblage across sites, we used a Redundancy Analysis (RDA). This ordination technique determines the relationship between species distributions patterns in site space and depicts the variation in the bird community that is constrained by the environmental attributes (ter Braak, 1986). We used Redundancy Analysis rather than Canonical Correspondence Analysis because the bird abundance was linear in response to the environmental constraints (ter Braak, 1986). Ordination analysis performs poorly when rare species are included, we eliminated species found at fewer than 10% of sites (McCune, Grace, & Urban, 2002).

We tested the overall significance for the RDA, each axis, and PCA components used in the analysis using a Monte Carlo Global Permutation Test (Hope, 1968). The total inertia of each RDA was used to measure the total variation in the community explained by habitat

and landscape components. We calculated bi-plot scores of the environmental constraints and factor loading for each species for the significant axes. We calculated guild centroids in ordination space by averaging the position of the species belonging to each guild. Finally, we generated a plot for each RDA to visually ascertain the relationship among waterbird community guilds and environmental variables.

We used generalized linear models (GLMs) to quantify the relationship between habitat and landscape components and waterbird community parameters (Nelder & Wedderburn, 1972). As was the case with the direct ordination, the independent variables used in the GLMs to describe habitat and landscape elements were the uncorrelated PCA components. For each response variable (guild abundance and diversity), we ran models for all the possible combinations of the habitat and landscape components as predictors, with a maximum of three components per model. We set the maximum number of predictors per model to three to keep a minimum of 10 observations per independent variable (the sample size was $n = 36$; Babyak, 2004). We used a Akaike Information Criterion, corrected for our small sample size (AICc), to select the most plausible models for each independent variable (Anderson & Burnham, 2002). AIC theory is based on a goodness of fit measure of candidate model i relative to the other models (Anderson, 2007). We selected all plausible models based on the threshold for $\Delta AICc_i$ scores, where the $\Delta AICc_i$ is the difference in the AICc value between candidate model i . A $\Delta AICc_i$ value of zero indicates the best performing model, and models with $\Delta AICc_i < 2$ are considered to be ecologically significant (McCallum, 2008).

3. Results

A total of 2679 individuals comprising 51 species of waterbirds were observed over the course of the study (Supplementary Material Table S1), with a maximum of 327 individuals per transect (Table 2). Richness at sites ranged from 1 to 29 species. The maximum number of individuals and species richness were observed at the Tres Rios Wetlands (33.3894, –112.2597). Fish-eating birds and dabbling ducks had the greatest number of species observed and rails had highest average abundance, with American Coot (*Fulica americana*) comprising 88.8% of the guild. Rare species were primarily found in areas of intermediate urban land use.

The Renyi Diversity Index showed perennial water with more emergent vegetation consistently exhibited higher diversity than large open sites, whereas diversity decreased in small, dry sites (Fig. 2). Similarly, intermediate levels of urbanization also displayed the highest levels of diversity, but by a closer margin than the gradient of water. However, diversity across levels of urbanization varied depending on the amount of water available (Fig. 3). In perennial sites, urban and intermediate land use were associated with higher H-alpha values, although this trend was reversed at drier areas (Fig. 3a vs. b).

Table 2

Descriptive statistics for bird guilds per site observed at 36 transects along the Salt River in Phoenix Arizona between the winters (December– February) of 2015 and 2016. Transects were placed along a gradient of water availability and urbanization. Species were assigned to foraging guilds according to Elphick & Dunning (2001). Species is the number of unique species observed within the guild. Mean abundance is defined as the total number of individuals (Total) observed per site.

Guild	Species	Total	Mean	SE	Range	
					Min	Max
Dabbling	11	564	15.66	4.33	0	111
Diver	8	542	15.05	4.04	0	80
Fish-eating	11	489	13.58	3.50	0	77
Rail	5	618	17.16	3.40	0	82
Shorebird	10	169	4.69	1.06	0	22
Wading	7	235	6.52	1.44	0	32

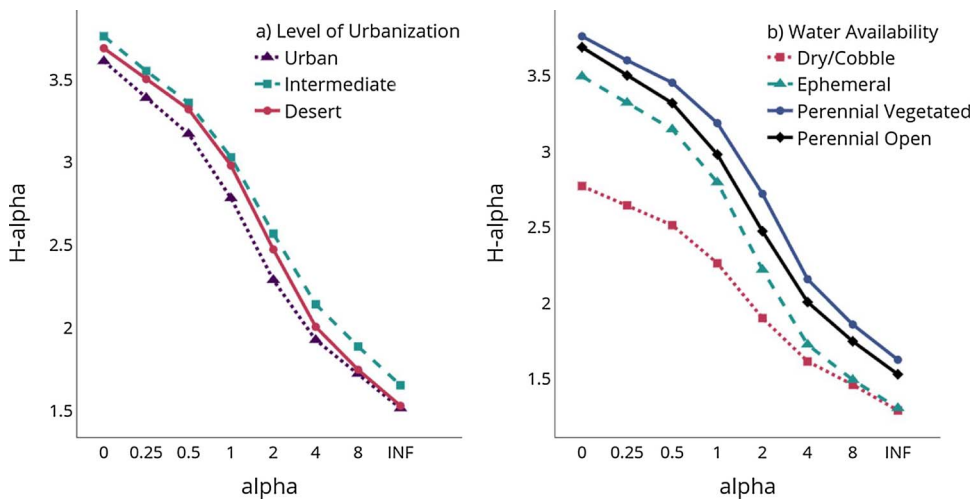


Fig. 2. Renyi diversity index (H-alpha) for waterbirds based on 36 sites surveyed along a gradient of water availability and urbanization between 2014 and 2016 in Phoenix, Arizona, USA. Horizontal axis (H-alpha) represents different discrete diversity indices that move from indices that place more emphasis on richness for lower values and abundance for higher values. a) Renyi index of sites grouped by urbanization gradient with n = 12 sites per group. Intermediate sites are the most diverse across all diversity indices. Desert sites exhibit higher H-alpha values than urban sites for indices placing an emphasis on richness, but are comparable using indices that place emphasis on abundance. b) Renyi index of sites grouped along water availability gradient in groups of n = 9. Sites that have intermediate levels of water availability but are vegetated exhibit higher diversity than open sites. Dry cobblebar sites have the lowest diversity.

3.1. Habitat and landscape components

The PCA analyses reduced 20 environmental variables to six components describing the main variation in habitat and landscape elements of the Salt River (Table 3). Twelve environmental variables were included in the habitat PCA; three components accounted for 74.5% of the environmental variation of habitat-level characteristics (Table 3). Habitat component C1 described vegetation and ground cover surrounding the water at the site. Sites with high C1 scores would exhibit high amount of canopy cover and greenness (NDVI), whereas lower C1 values represented more impervious surface and less vegetation (Table 3). High and low values of component C2 were inverted for interpretation purposes. Sites with high component C2 scores had large areas of open water with an ample amount of artificial structures for perching, whereas low C2 scores described habitat that has less water and is drier overall (Table 3). Sites with high C3 scores were defined by shoreline complexity and emergent vegetation (Table 3). The components were renamed for reference purposes based on their interpretation: C1-Vegetation, C2-Water Physiognomy, and C3-Shoreline (Table 3).

The landscape PCA reduced eight variables into three components explaining 85.2% of the variability in the landscape surrounding the surveyed riparian areas (Table 3). Component C4 represented a gradient from desert habitat (high scores) to highly urbanized matrix (low scores). High component C5 scores corresponded to areas in Phoenix located in intermediate disturbance zones, close to adjacent agriculture fields and cultivated vegetation (Table 3). Component C6 was inverted

for interpretation and analysis. Sites with high C6 scores had a large amount of water resources in the landscape (1.5 km). The landscape components were renamed based on their variable loadings: C4-Desert, C5-Agriculture, and C6- Landscape water (Table 3).

3.2. Community composition

The RDA explained a proportion of waterbird community variation greater than expected by chance ($F_{5,30} = 3.82, P < 0.001$). The first two axes of the ordination were significant ($F_{1,32} = 11.75, P < 0.001$; $F_{1,32} = 4.96, P < 0.001$; Fig. 4). In total, the components explained 38.9% of the variation of the waterbird community in Phoenix, Arizona along the Salt River.

There was a strong gradient of habitat-level water characteristics represented along the RDA1 axis of the habitat ordination driven by the Water Physiognomy and Vegetation components. Extent and openness of water at a site decreased when moving from low to high RDA1 axis values, whereas terrestrial vegetation and greenness increased. RDA2 denoted a gradient of land use and the shoreline component. Increased RDA2 axis values represented a shift from low levels of emergent vegetation into more complex areas with a dominant shoreline, providing more shallows and vegetation access along the edge. A strong land use gradient, from urban to desert, was also described with increased RDA2 values. The upper left quadrant of the ordination included large, open desert sites with low amounts of terrestrial and emergent vegetation; the lower left quadrant included wet vegetated sites with complex shoreline and agricultural land use; the bottom right quadrant was

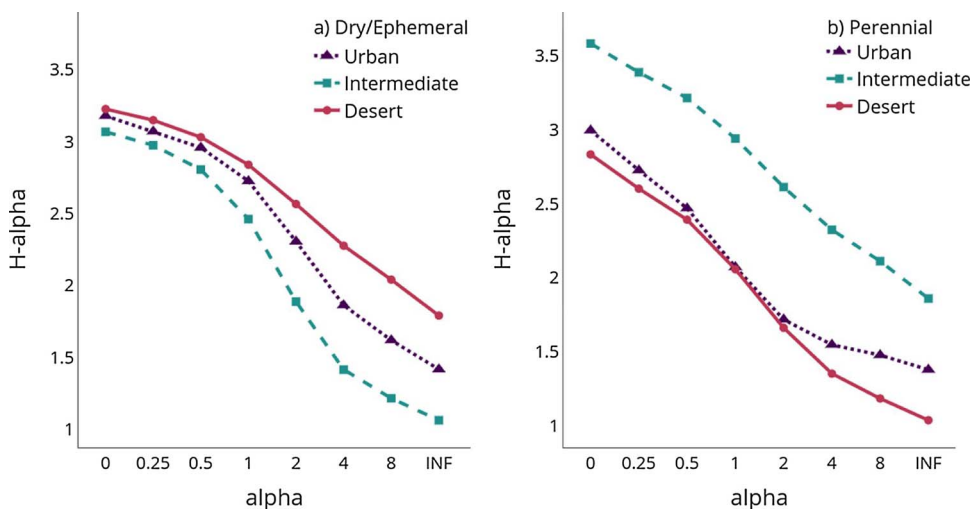


Fig. 3. Renyi diversity index of urbanization gradient for subsets of, a) sites within the lowest two quartiles of water availability (n = 18), and (b) sites within the upper quartile of water availability (n = 9). In dry sites, a), the desert has the highest levels of diversity, but this trend is reversed in sites with large amounts of water, b). Urban and intermediately developed sites with perennial water exhibit higher H-alpha values across indices when compared to desert sites.

Table 3

Results from two separate Principal component analyses (PCA) of environmental variables, The Habitat PCA based on 12 variables describing habitat (aquatic and terrestrial), and the Landscape PCA based on 8 variables describing landscape characteristics along 36 Salt River transects in Phoenix, Arizona. Each PCA yielded three components, and together these six components were used as the explanatory variables for analysis. Variables with the highest loading for the respective component are shown in bold.

Habitat PCA			
	C1 Vegetation	C2 Water Physiognomy	C3 Shoreline
Tree/shrub	0.41	0.00	−0.13
Canopy cover	0.35	0.02	−0.02
Impervious surface	−0.35	−0.22	0.23
NDVI	0.30	0.16	0.00
Open water	−0.20	0.45	−0.13
Extent	−0.30	0.37	−0.06
Perching structure	−0.17	0.36	0.30
Bare ground	−0.13	−0.46	0.11
Connectivity	−0.23	−0.41	0.24
Emergent vegetation	0.33	0.10	0.50
Edge ratio	0.36	−0.05	0.39
Cobblestone	0.15	−0.25	−0.58
Variation Explained (%)	37.63	28.27	8.65
Eigenvalue	4.52	3.39	1.03
Landscape PCA			
	C4 Desert	C5 Agriculture	C6 Landscape Water
Urban	−0.50	−0.24	0.08
Distance to desert	−0.49	−0.18	0.06
Isolation	−0.39	−0.21	−0.34
Distance to agriculture	0.39	0.43	−0.10
Cultivated vegetation	−0.21	0.47	0.40
River gravel	−0.17	0.52	0.05
Landscape-scale water	0.18	−0.25	0.71
Riparian vegetation	0.31	0.35	−0.44
Variation Explained (%)	40.16	28.45	16.53
Eigenvalue	3.21	2.28	1.32

composed of dry, disturbed habitat, and the upper quadrant indicated desert sites with prominent cobblestone (Fig. 4).

All three habitat components were significant in explaining waterbird community assemblage patterns: Water Physiognomy ($F_{1,32} = 8.73$, $P < 0.001$), Vegetation ($F_{1,32} = 3.40$, $P < 0.002$) and Shoreline ($F_{1,32} = 3.03$, $P < 0.010$). The Water Physiognomy vector was tightly aligned with birds that dive for their food. Diving ducks and fish-eating birds concentrated at areas that corresponded to high Water Physiognomy vector values, indicating association with large, open bodies of water (Fig. 4). Rails, wading birds, and dabbling ducks fell at the lower end of the RDA2 gradient and were associated with more complex, vegetated shoreline (Fig. 4). The mean position of shorebirds was found at high values of RDA1 and intermediate values of RDA2, contrasting with the other guilds in their position on the ordination (Fig. 4).

The variation in the waterbird community in Phoenix, Arizona was also defined by two of the landscape components included in the ordination, Agriculture ($F_{1,32} = 1.96$, $P < 0.035$) and Desert ($F_{1,32} = 2.01$, $P < 0.039$). However, contrary to our hypothesis, landscape-scale water was not significant in structuring the community. Dabbling ducks, wading birds, and rails were associated with higher levels of urbanization and agriculture. Conversely, diving ducks were negatively related to urbanization, but were found in similar reaches as fish-eating birds (chiefly driven by the water physiognomy component vector). In support of the Renyi Index results, dry urban sites (high RDA1 and low RDA2 values) lacked association with any of the guilds, whereas both perennial and ephemeral agricultural and urban sites

structured community composition of multiple guilds.

3.3. Abundance and diversity

The best fit models that were selected by AICc emphasize the role of habitat components in predicting waterbird guild abundance and diversity (Table 4). Water physiognomy was especially important, as was expected in an arid climate, and was included in all but two of the top ranked models. Comparatively, level of development was only selected in five of the models, with urbanization being positively associated with dabbling ducks, fish eating species, wading birds and overall diversity. Our results support that the waterbird community is largely responding to local habitat elements and that heterogeneous patches throughout the urban matrix support an abundant, but diverse suite of species.

Wading birds were the only guild that did not include water physiognomy in their best-fit model, instead species largely responded to vegetation and agricultural land use components, both of which provided terrestrial foraging resources. Dabbling ducks were associated with complex shoreline and emergent vegetation dominating the littoral zone. The best-fit model for dabbling ducks included water physiognomy and shoreline components. Diving ducks were the only guild negatively associated with urbanized areas and also avoided sites with vegetation around the shoreline. Fish-eating species were very similar to diving ducks in locally selected habitat components, but were positively related to human development. Rallidae species (primarily American Coots) were positively associated with the shoreline component, as well as water physiognomy. American Coots (Rail guild) were also the sole guild to be positively associated with the landscape water component. Shorebirds were the only guild to decrease abundance with increasing water area, and instead selected habitat with cobblestone and more ephemeral water sources to forage.

4. Discussion

Waterbirds use both traditional and human-built habitat throughout the urban matrix in Phoenix, Arizona, USA. We found that the physical patch structure, referred to as water physiognomy, was the strongest driver shaping waterbird community parameters in an arid city. Level of urbanization did not affect richness or diversity, but did affect community composition, with specific foraging guilds being associated with different land use types. Overall, our study highlights the potential of urban riparian corridors to provide waterbird habitat. The results of our study should be taken into consideration as areas with water are created, removed, or restored within an urban landscape.

4.1. The importance of habitat structure

The shape and size of aquatic habitat is a well-established driver of waterbird abundance and diversity in non-urban systems (Froneman, Mangnall, Little, & Crowe, 2001; Rosa, Palmeirim, & Moreira, 2003; Sánchez-Zapata et al., 2005). We used the importance of aquatic habitat for waterbirds to postulate that abundant water resources in Phoenix offset some of the negative effects of anthropogenic pressure. For example, we found that dry urban areas have lower levels of biodiversity compared to the outlying desert, but where water is abundant, urbanized areas have higher levels of diversity than the desert.

The habitat features of a given patch were more important than the surrounding matrix, indicating that waterbirds are responding to the heterogeneity of fine scale habitat in arid cities instead of surrounding level of urbanization. A potential explanation is that adjacent and well-connected wetlands, or wetland 'clusters', in urban landscapes function similarly to the larger wetland patches in undeveloped landscapes (Pearce, Green, & Baldwin, 2007). However, other studies have shown that, contrary to our findings, anthropogenic development near urban lakes and estuaries has negative impacts on waterbird communities (DeLuca, Studts, Rockwood, & Marra, 2004; Murray, Kasel, Loyn,

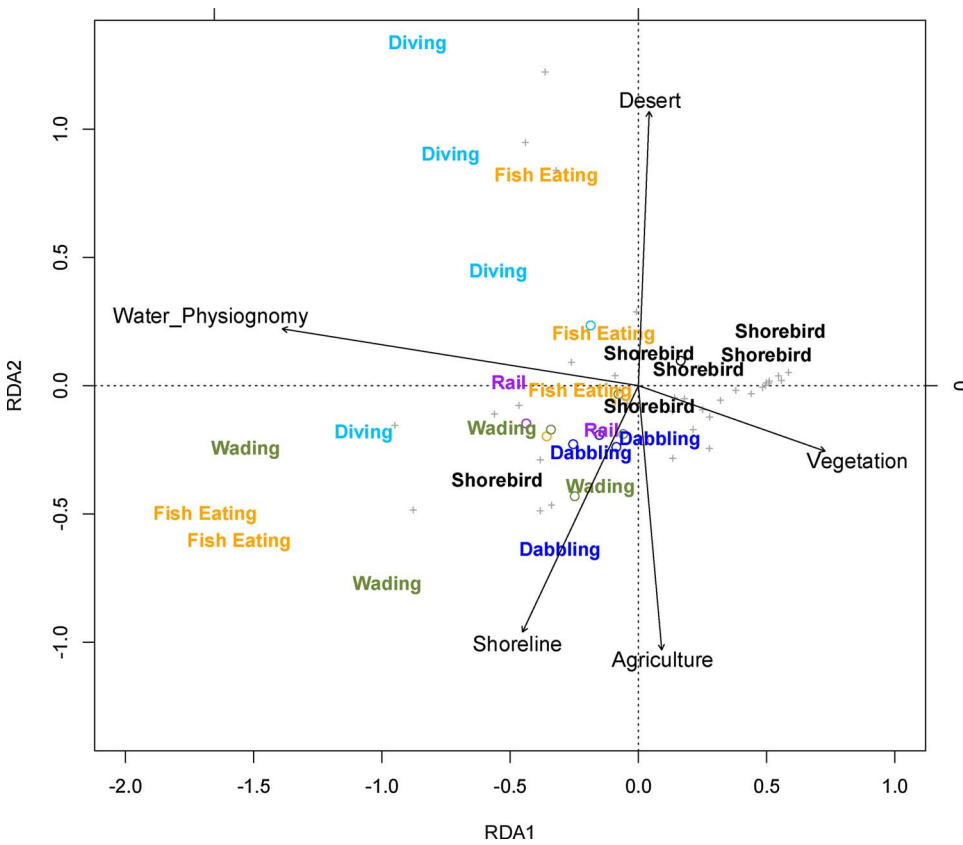


Fig. 4. RDA ordination diagram of waterbird species, labeled by guild, constrained by habitat and landscape PCA components at 36 sites in Phoenix, Arizona. The ordination explained 38.9% of the variation found in the waterbird community. Species in close proximity to each other in ordination space are likely to be found at similar sites. Component vectors closer to one another indicate conditions that covary, and the length of the vector indicates the correlation value strength between component and community composition. Dabbling ducks are represented by purple, diving ducks by light blue, fish-eating birds by dark blue, wading birds by tan, rails by green, and shorebirds by orange. Component vectors are labeled as in Table 3: (C1) Vegetation, (C2) Water Physiognomy, (C3) Shoreline, (C4) Desert, (C5) Agriculture, and (C6) Landscape Water. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4

Environmental components used to predict waterbird guild abundance and diversity in Phoenix, Arizona (n = 36 transects) using AICc ranked models. The top competing models with $\Delta AICc < 2$ are listed as ranked, with lower $\Delta AICc < 2$ representing models that have more support in predicting the response variable. The standardized beta estimate (β) represents the strength and directionality of the relationship between habitat and landscape components and community response in the top-performing model for each community metric. Components are (as in Table 3): (C1) Vegetation, (C2) Water Physiognomy, (C3) Shoreline, (C4) Desert, (C5) Agriculture, and (C6) Landscape Water.

Guild	Model	AICc	$\Delta AICc$	ω	Habitat (β)			Landscape (β)		
					C1	C2	C3	C4	C5	C6
Dabbler	C2 + C3	-127.8	0.00	0.31		0.45	0.44			
Dabbler	C2 + C3 + C5	-126.8	0.99	0.19		0.46	0.41		0.17	
Dabbler	C2 + C3 + C4	-126.8	1.71	0.12		0.50	0.36	-0.16		
Diver	C1 + C2 + C4	-113.3	0.00	0.35	-0.34	0.46		0.39		
Fish-eating	C1 + C2 + C3	-171.2	0.00	0.47	-0.49	0.65	0.23			
Fish-eating	C1 + C2 + C4	-170.5	0.65	0.34	-0.39	0.73		-0.25		
Rail	C2 + C3 + C6	-83.19	0.00	0.20		0.30	0.27			0.36
Rail	C2 + C6	-82.07	1.12	0.11		0.30				0.35
Rail	C3 + C6	-81.77	1.42	0.10			0.27			0.47
Shorebird	C1 + C2	-145.7	0.00	0.17	0.36	-0.33				
Shorebird	C1 + C2 + C5	-145.1	0.68	0.12	0.42	-0.35			-0.21	
Shorebird	C1 + C2 + C3	-144.1	1.66	0.08	0.35	-0.33	-0.15			
Wading	C2 + C4 + C5	-151.0	0.00	0.38	0.47			-0.33	0.44	
Shannon	C1 + C2 + C4	47.34	0.00	0.43	0.41	0.81		-0.27		
Shannon	C1 + C2 + C3	48.81	1.46	0.20	0.29	0.71	0.20			
Richness	C2 + C3	199.4	0.00	0.34		0.80	0.27			
Richness	C2 + C3 + C5	200.9	1.59	0.15		0.81	0.25		0.10	

Hepworth, & Hamilton, 2013; Rajashekara & Venkatesha, 2011; Žydelis & Kontautas, 2008). One potential explanation for the discrepancy between our study and others is the redistribution of water in certain arid cities interacting with the requirements of our study taxa. Therefore, the effects of anthropogenic development on waterbirds may be expected to vary depending on climate.

The development of Phoenix has, perhaps counter-intuitively, increased the total water permanence throughout the city when compared to the surrounding desert. This helps explain how Phoenix's discrete blue spaces are able to subsidize such high levels of waterbird

diversity and abundance. As long as the local habitat feature has the characteristics needed to support the community, features of the surrounding urban matrix are relatively unimportant. Additionally, the heterogeneity of patches throughout the urban gradient was able to provide different habitat for different foraging guilds. Instead of a continuous but homogenous corridor, the Salt River in Phoenix is now a mixture of habitats from perennial lakes to dry cobblestone, supporting a wider range of foraging and habitat requirements. Similarly, Banville, Bateman, Earl, and Warren (2017) found that riparian areas characterized by water permanence in the Salt River supported more

passerines and other terrestrial birds than ephemeral or dry reaches, whether or not a site was human-built habitat.

4.2. Management implications

The presence and construction of lakes and wetlands in urban environments is important for biodiversity conservation as urban areas continue to expand and natural wetlands decline (Zedler, 2000). Urban water that is properly managed can provide habitat with the capacity to support biodiversity. Phoenix alone contains over 1400 urban lakes, as well as stormwater drainage basins, gravel pits, and treatment ponds that provide recreational areas or other public amenities as part of the urban infrastructure (Larson & Grimm, 2012). Waterbird conservation is not always the focus of the built habitat, but seems to be an unintended consequence of many urban wetlands. Here we show that waterbirds are taking advantage of the water in Phoenix and that the heterogeneous habitat patches within the urban matrix can be beneficial for supporting regional diversity by providing vital resources to a variety of species.

Our study suggests that urban water in Phoenix provides an important subsidy for migrating waterbird communities. Areas such as the Tres Rios Wetlands (constructed wetlands for wastewater treatment) and the Rio Salado Restoration Area (a public space with hiking and recreational opportunities) are both excellent examples of how water resources along the Salt River can serve both the community and urban wildlife (Banville et al., 2017). It is also interesting to consider some of the potential outcomes if the “leakiness” of storm drains is improved or the amount of public water is reduced (Chocat, Marsalek, Matos, Rauch, Schilling, & Urbonas, 2007; Archibold, 2007). As water conservation becomes increasingly important (Hirschboeck & Meko, 2005), there must be awareness that water is a multi-faceted resource with the potential to optimize habitat and support biodiversity in addition to providing public services (Hansson, Brönmark, Anders Nilsson, & Åbjörnsson, 2005; Ignatieva, 2010). Biodiversity provisioning is often one of the overlooked, but important, ecosystems services that urban blue space provides.

4.3. Future directions

Temporally, our study was conducted in two wet El-Niño years; observations collected during drier winters may reflect different degrees of interaction between waterbirds and their environment. However, we expect that drier years would make the findings on the importance of water and productivity inside cities more pronounced, not less. Additionally, the unique water dynamics of arid cities may also cause conflicting results if compared to a similar study done in a less-arid climate. A long-term, multi-city approach would help determine what trends hold true globally, while maximizing localized conservation knowledge.

5. Conclusion

This study indicates that water resources in Phoenix are capable of supporting large, diverse waterbird communities. Our study also provides several insights into the links between habitat and landscape structure and waterbird community patterns in an arid city. Water shape and size at the habitat-level is important to waterbird abundance and diversity, whereas the intensity of urbanization and landscape-level water are less important. Land use shapes the suite of species at each site, but is not related to overall abundance or diversity, supporting the hypothesis that urban water can support healthy waterbird communities if managed correctly.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.landurbplan.2017.11.003>.

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