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Research article

Wintering waterbird community responses to anthropogenic land cover at multiple spatial scales along the Nile in Egypt

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Wildlife Biology
2024: e01178
doi: 10.1002/wlb3.01178

Subject Editor: Bogdan Cristescu
Editor-in-Chief: Ilse Storch
Accepted 24 August 2024

The human population is growing rapidly, increasing pressure on natural habitats. Suitable habitats for resident and migratory waterbirds are, therefore, more threatened. This study analyses how the presence of anthropogenic land cover (urban area and cropland) at multiple spatial scales affects the community composition of waterbirds along the Nile in Egypt. We analysed data collected during the international waterbird census, 2017–2018, combined with data from satellite images on land cover from the same period. The census covered 970 km, compromising 194 transects of 5 km along the River Nile, Egypt. The area includes a broad gradient of human disturbance, making this dataset ideal for assessing effects of anthropogenic land cover on waterbird community composition. We tested whether the waterbird community indices (abundance, species richness, diversity and evenness) and guild composition were associated with urban area and cropland, and other land covers (e.g. grassland, wetland) at spatial scales of 100, 500, 1000 and 5000 m. We recorded over 96000 waterbirds and show that landscape characteristics at larger spatial scales (5000 m) explained more of the species and guilds' presence than smaller scales. Species richness increased with increasing water surface area of the river within the transect and decreased with increasing urban area. Waders were negatively associated with urban area. Overall, the guilds' composition was poorly predicted by anthropogenic land cover and other landscape compositions, probably because species within a guild do not react similarly to increasing human disturbance. The probability of observing red-listed species decreased with increasing urban area. With this study, we expand on the existing evidence by showing that species richness negatively correlates with anthropogenic pressure, and we highlight the importance of studying the responses of species rather than guilds. Our study shows the relevance of considering the landscape at larger scales (5000 m) while planning for conservation measures.

Keywords: anthropogenic land cover, community composition, guild, multi-spatial scale, River Nile, waterbird

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Introduction

The human population has been growing rapidly in recent decades, leading to a strong increase in anthropogenic pressure on natural habitats. Human settlement expansion over or next to natural habitats is currently one of the leading causes of biodiversity loss (Pimm and Raven 2000, Cincotta and Gorenflo 2011, Rigal et al. 2023). Animal species vary in their tolerance to such environmental changes and human disturbance. Thus, understanding the effects of these anthropogenic pressures on animal communities is key for understanding drivers of species distributions, prioritising conservation measures, and making valid predictions about population and community trends (Granadeiro et al. 2007, Liordos 2010). In animal communities, some species groups are more sensitive to disturbance than others, and therefore they can be used as biological indicators to assess environmental changes (Ogden et al. 2014). Specifically, waterbird communities are sensitive to changes in their environment and are thus suitable candidates for studying the effects of environmental change and human disturbance on ecosystems (Ma et al. 2010, Alexander and Hepp 2014).

Although birds are among the species groups with a high proportion of species assessed as Least Concern, according to the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species, about 55% of the world's waterbird species are declining. Moreover, 17% of waterbird species have been listed as threatened in the Red List (BirdLife International 2017). Habitat loss, human disturbance, environmental pollution and illegal hunting are considered important causes of waterbird declines across the globe (Delany 2010b, Zöckler 2012, Wang et al. 2018). One of the main reasons for the decline in migratory bird populations, many of which are waterbirds, is the decline in habitat quality at their wintering grounds and stopover sites, which are essential for survival (Newton 2006, Xu et al. 2019).

Local habitat characteristics, such as habitat type, vegetation cover and water quality can influence the presence of species. Moreover, human disturbance, for example natural habitats are converted to anthropogenic land cover (i.e. urban area or cropland), can lead birds to occupy less suitable habitats (Mathers and Montgomery 1997, Carney and Sydeman 1999). Subsequently their distribution patterns can change, which affects their reproduction and survival (Pearman 2002, Burton et al. 2006, Barbaro et al. 2007). The conversion of natural ecosystems to land with a high human footprint can have large negative impacts on birds, yet some species can benefit (Delany 2010b).

The extent and direction of the impacts of human presence depend on the species. For instance, several heron and egret species can benefit from human presence by foraging on garbage or in cropland (Chace and Walsh 2006). Other species are negatively affected by human presence, such as wader species that lose their suitable habitats due to construction on shorelines in urban area (Ruhlen et al. 2003, Van der Kolk et al. 2022). The transformation of sand bars and mudflats into cropland can negatively affect small wading species, while it might offer suitable habitats for geese and dabbling ducks (Tavares and Siciliano 2013, Jedlikowski et al. 2014). Some species have started to adapt to human presence, such as the Eurasian oystercatcher *Haematopus ostralegus*, originally a coastal bird that breeds in salt marshes, that now started breeding on flat roofs in cities (Duncan et al. 2001, Ens et al. 2011). For yet other species, it is still unclear how, and to what extent, they are affected by human disturbance. Such responses to human presence affect the patterns of species presence and thereby the species assemblage structure. It is thus vital to better understand the effects of human disturbance, including the presence of anthropogenic land cover, on species to get more comprehensive insights into specific anthropogenic drivers of species distribution, and so benefit species conservation (Gillespie et al. 2008, Walz 2011, Schindler et al. 2013, Adler and Jedicke 2022). However, species with large home ranges can be affected by landscape characteristics over different spatial scales, such as the presence of urban area, cropland, or wetland (Westphal et al. 2003, Morrison et al. 2006, Borges et al. 2017). Since species respond differently to local versus landscape-level characteristics, species distribution patterns should be assessed across multiple spatial scales (Mayor et al. 2009).

Here we determined the link between the presence of anthropogenic land (defined here as urban area and cropland) and the distribution of waterbird communities at multiple spatial scales along the Nile in Egypt. We focused on this region for a number of reasons. About 90% (more than 90 million people) of the human population of Egypt is concentrated along the Nile in an area of about 5% of the total area of the country (50 000 km^2). The fast human population growth rate of Egypt of about 1.9 % per year clearly illustrates the rapid expansion of anthropogenic land cover. The Nile Valley is a linear mosaic of different types of habitats located in the middle of an unhospitable matrix, the Sahara. Moreover, the Nile is a vital migration corridor linking the Mediterranean Sea region to sub-Saharan Africa, providing critical wintering grounds and stopover sites for waterbirds. Its broad gradient of anthropogenic land cover thus offers an ideal opportunity to quantify how habitat and landscape characteristics related to human presence affect waterbird community composition. Since river ecosystems, such as the Nile, are essential areas for humans as well as birds, a rapidly growing human population leads to increasing anthropogenic pressures on natural habitats. Suitable habitats for waterbirds are threatened, and these anthropogenic stressors might negatively impact the resident and migratory bird species, which depend on those habitats as wintering and stopover sites. The question is to what extent anthropogenic land cover at different spatial scales can explain the variation in waterbird community composition in this region.

The aim of this study was to determine the relationship between anthropogenic land cover and waterbird communities at multiple spatial scales. We also examined responses to different landcover classes, including the anthropogenic land cover (urban area and cropland), at guild level; a guild is a

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group of species with similar niche requirements which may respond similarly (Simberloff and Dayan 1991). We expected that transects with less anthropogenic land cover in the surrounding landscape would host more bird species from more guilds with overall a richer bird community. Moreover, we predicted that the transects surrounded by urban area (highly disturbed areas) have relatively poor communities, i.e. communities with low species richness and diversity, with more herons, egrets and gulls, and some raptor species, but fewer waders and deep-water feeding species. We further expected that higher water availability at larger spatial scales (e.g. nearby sewage ponds and irrigation canals) would lead to more species, larger numbers and a higher diversity of waterbirds. A larger surface of the Nile within a transect as well as the shoreline length are expected to positively affect the species richness and abundance of waterbirds. We also predicted that the probability of detecting red-listed species decreased under human influence. We expected the heterogeneity of land cover classes in the surrounding landscape to affect the species richness positively.

Material and methods

Study area and field survey

The data from the International Waterbird Census (winter 2017/2018) used in this study was collected by the first author together with a team of four researchers of the Egyptian Environmental Affairs Agency, all experienced in identification of wintering waterbirds in the River Nile. Here, suitable habitats for both waterbirds and people are aligned along the narrow (ranging from 700 m to 20 000 m) Nile Valley (Baha El Din 1999). The seasonal water level fluctuates at an average of 15 m and creates temporally suitable habitats of sandbanks and mudflats, which are used by waterbirds in winter (Goodman and Meininger 1989). The data was collected along 194 adjoining 5 km long transects on the River Nile between Aswan and Cairo, over a distance of about 970 km (Fig. 1). A transect of 5 km long was deemed a suitable scale to be able to generate representative data from the target area and provide relatively fine scale details. Two teams of at

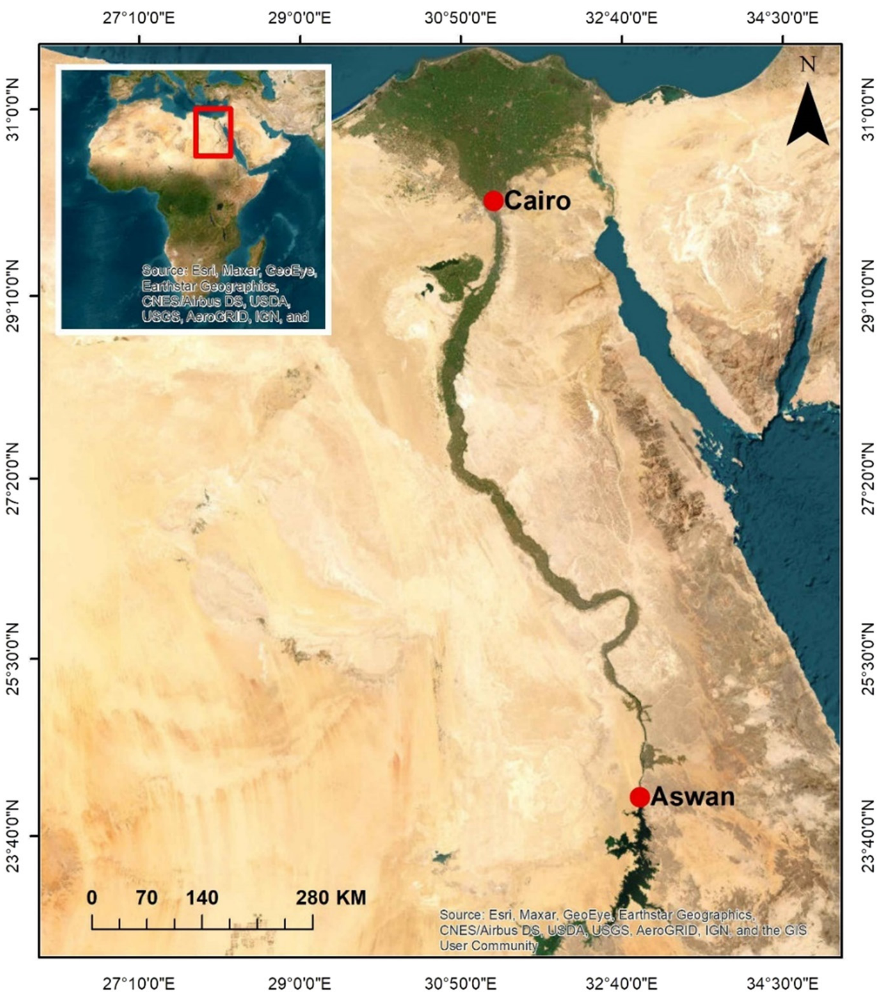

Figure 1. Study area showing the River Nile and the start and end points (Aswan and Cairo) in between which the 194 transects were surveyed in winter 2017/2018 (Source: ESRI Maxar. Geo Eye, Earthstar Geographics, CNES/Airbus D6, USDA, USGS, AeroGRID, IGN & GIS User Community)

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least two observers, using (10 × 42) binoculars and (20 × 60) spotting telescopes, were involved in the survey. Data of all waterbirds and raptors were collected using a small local motorboat moving along the centre of the Nile at an average speed of 8 km h^{-1}. Both stationary birds and birds flying over were counted on both sides of the river and were summed per transect (Bibby et al. 1998, Delany 2010a). In some parts of the study area, the river was wide, making it difficult to identify some bird individuals on the shores, such as small-sized waders. Therefore, we grouped those individuals into: wader sp., duck sp. and marsh terns and included them in the guild analysis. The survey took 14 days in the period 27 December 2017 – 9 January 2018, starting one hour after sunrise and finishing one hour before sunset. Weather conditions were stable with no rain or major wind during the field survey, so we did not include weather parameters in the analyses. The time of the day of the survey was not correlated with species richness, abundance or diversity, and was therefore also omitted from the analysis.

Land cover data extraction

We used the S2 Prototype Land Cover 20m map of Africa (ESA Climate Change Initiative – Land Cover project 2017), which is based on 1 year of Sentinel-2A observations from December 2015 to December 2016, to extract environmental predictor variables. We quantified the characteristics of each transect and the land cover in the surrounding landscape. For each transect, we defined the polygon of the River Nile which contained the 5 km transect. Then we calculated 1) the water surface area of the river and 2) the shoreline length. Moreover, we used the satellite image to quantify the surrounding landscape characteristics at multi-spatial scales (100, 500, 1000, 5000 m), here referred to as buffers. Buffers were drawn parallel to both shorelines of the River Nile in the area where the 5 km transect was located. Different buffer sizes were used to assess the effect of landscape characteristics on the community composition of waterbirds which were observed in the Nile during the survey. The 100 m buffer is used to assess the land cover within the immediate vicinity of the river, while larger scales of 1000 and 5000 m used to capture the landscape characteristics further away from the river. The landscape characteristics include the land covers (3) tree, (4) shrub, (5) grassland, (6) cropland, (7) wetland, (8) sparse vegetation, (9) bare land, (10) urban area, and (11) deep water (Table 1). We used QGIS 3.16 (QGIS Development Team 2020. QGIS Geographic Information System. Open Source Geospatial Foundation Project http://qgis.osgeo.org) for buffering and land cover data extraction. We used the normalised difference vegetation index (NDVI) of water in the Nile as an indicator to water clarity due to presence of aquatic vegetation, algae, or other materials (Fan et al. 2020). Moreover, we used the NDVI of the surrounding buffer area at all spatial scales as an indicator of vegetation cover and heterogeneity in the surrounding landscape. Mean and SD of the NDVI of water in the Nile (12, 13) and mean and SD of the NDVI in buffers (14, 15) were calculated using Sentinel-2 wide-swath, high-resolution (10 m), multi-spectral data (Red and near Infrared bands) filtered to the period of bird data collection (1 December 2017 – 31 January 2018). We used Google Earth Engine for the extraction and calculation process of NDVI (Gorelick et al. 2017). To account for a potential positive effect of habitat heterogeneity, we also calculated (16) an index of the heterogeneity of land cover classes (i.e. Shannon–undefinedWiener diversity index H′ for land cover classes).

Data analysis

We calculated community composition indices of waterbirds for each 5000 m transect, including (1) abundance (i.e. total number of birds) (2) species richness (i.e. number of species) (3) species diversity (Shannon–Wiener diversity index H′), and (4) species evenness (H′/ln species richness). Species were categorised into seven different guilds based on their dominant foraging habitats and behaviour: (1) dabbling ducks and gallinules, (2) diving birds and deep-water feeders, (3) gulls, (4) open-water fishing birds, (5) raptors, (6) stalking herons, ibises, and storks, and (7) waders. Furthermore, we reported the presence/absence (binary, 0/1) of red-listed species for

Table 1. Environmental variables and their spatial scale.

Variables	Explanation	Spatial scale
(1) Water Surface	The water surface area of the river	Local/transect
(2) Shoreline	Shoreline length of the river	Local/transect
(12) MNDVI.W	Mean of NDVI of water in the Nile	Local/transect
(13) SDNDVI.W	SD of NDVI of water in the Nile	Local/transect
(3) X1	Tree cover	Landscape/buffers:100, 500, 1000, 5000 m
(4) X2	Shrub cover	Landscape/buffers:100, 500, 1000, 5000 m
(5) X3	Grassland cover	Landscape/buffers:100, 500, 1000, 5000 m
(6) X4	Cropland cover	Landscape/buffers:100, 500, 1000, 5000 m
(7) X5	Wetland cover	Landscape/buffers:100, 500, 1000, 5000 m
(8) X6	Sparse vegetation cover	Landscape/buffers:100, 500, 1000, 5000 m
(9) X7	Bare land cover	Landscape/buffers:100, 500, 1000, 5000 m
(10) X8	Urban area cover	Landscape/buffers:100, 500, 1000, 5000 m
(11) X10	Deep water cover	Landscape/buffers:100, 500, 1000, 5000 m
(14) MNDVI	Mean of NDVI	Landscape/buffers:100, 500, 1000, 5000 m
(15) SDNDVI	SD of NDVI	Landscape/buffers:100, 500, 1000, 5000 m
(16) H′ land cover	Land cover diversity index (Shannon–Wiener diversity index H′)	Landscape/buffers:100, 500, 1000, 5000 m

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each transect (IUCN Red List categories: near threatened (NT), vulnerable (VU), endangered (EN), and critically endangered (CR)).

We analysed the effects of the environmental variables and anthropogenic land cover on waterbird community composition using regression analyses with the relative composition of each of the guilds, the abundance, evenness, and diversity as response variables. Assumptions underlying the regression analyses for a Gaussian distribution were verified by testing residuals for normality and heteroscedasticity. For the analysis of the species richness data, we used a generalized linear model, with a Poisson distribution. Prior to these analyses, we determined the best-fitting spatial scale per environmental variable based on the highest absolute correlation coefficient for each dependent variable. For the analysis of the probability of reported red-listed species we used a binary logistic regression. All analyses were carried out with a forward selection ($p < 0.05$) of predictors, starting with the most significant predictor. Two of the environmental variables at 5000 m spatial scale (mean NDVI and bare land cover) were highly collinear with cropland cover (correlation coefficient > 0.8) and were therefore omitted from the regression analyses. These analyses were performed using the IBM SPSS statistics for windows, ver. 28.0.

We carried out a principal component analysis (PCA) to analyse the guild-level community composition in relation to anthropogenic and environmental variables using Canoco ver. 5.0. Response data were compositional and covered a gradient 2.6 SDs, justifying the use of the PCA (Šmilauer and Lepš 2014). Subsequently, we ran a constrained redundancy analysis to determine the impact of the most important explanatory variables. PCA and RDA were run on log-transformed data (Šmilauer and Lepš 2014).

Results

A total of 96 058 individuals, 66 waterbird species and seven guilds were recorded during the survey of the River Nile (about 970 km) between Aswan and Cairo (Fig. 1). Species richness per transect ranged between six and 38 species, while bird abundance ranged between 28 and 10 743 birds. The species diversity index H′ ranged between 0.3 and 3.3, i.e. from low to high diversity. Most recorded individuals belonged to the dabbling ducks and gallinules guild, with a total of 25 907 individuals recorded in 178 transects (92%), while only 227 individuals recorded in 109 transects (56%) were raptors. Stalking herons, ibises and storks were recorded in every transect, but diving birds and deep-water feeders appeared in only 100 transects (52%) (Table 2).

Community composition and landscape characteristics

Species richness was associated with the water surface area of the river and the NDVI of water in the Nile, with more species in transects with larger water surface areas and lower NDVI. Moreover, the landscape variables at a spatial scale of 5000 m explained significantly more of the variation in species richness than at smaller spatial scales (Table 3). The anthropogenic land cover (i.e. urban area) associated negatively with species richness. The variation of the NDVI at the 5000 m spatial scale, reflecting the variation in vegetation, also associated negatively with species richness (Fig. 2).

Table 2. Bird abundance, number of species and percentage of occurrence per guild type in the transects (n = 194).

Guild	Abundance	No. of species	% of occurrence in transects
Dabbling ducks and gallinules	25 907	11	91.75
Diving birds and deep-water feeders	17 352	6	51.55
Gulls	3809	4	58.25
Open water fishing birds	15 552	10	96.91
Raptors	227	5	56.19
Stalking herons, ibises and storks	23 028	13	100
Waders	10 183	18	89.18
Total	96 058	66	

Bird abundance associated positively with the water surface area of the river, yet associated negatively with the variation of the NDVI of the water in the Nile, while it was not affected by any of the landscape variables around the Nile. The other measures of community composition, species evenness and diversity, were related to different combinations of environmental variables. The species evenness was positively correlated with the variation of NDVI of water in the Nile and negatively with tree cover in the 5000 m buffer. The diversity index was positively correlated with the water surface area of the river of a transect and negatively with the variation of the NDVI in the 5000 m buffer. The length of the shoreline was not correlated with any of the response variables.

Distribution of different bird guilds in relation to landscape characteristics

The abundance of individuals in each of the seven guilds was associated with different combinations of water and landscape variables (Table 4, Fig. 3). The number of dabbling ducks and gallinules did not correlate with any of the measurements of the Nile in a transect, but correlated negatively with grassland in the 100 m buffer and wetland in the 5000 m buffer. The number of diving birds and deep-water feeders, in contrast, associated positively with water surface area of the river and negatively with SD of NDVI of water in the Nile. The gulls also did not correlate with any of the variables of the Nile itself but were positively correlated with wetland in the 5000 m buffer and negatively with deep water in the same buffer. The open-water fishing birds decreased with the increase of mean NDVI of water in the Nile and increased with urban area in the 1000 m buffer. Raptors showed a positive association with shoreline length, shrub cover in the 100 m buffer, wetland cover in the 5000 m buffer, and SD of NDVI in the 5000 m buffer. Stalking herons, ibises and storks were

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Table 3. Regression analysis results (standardised regression coefficient B; t-value; p-value; R^2 adjusted, n = 194) to predict the effect of different variables on abundance, evenness, and the Shannon diversity index H′. For species richness a generalized linear model was used with a Poisson distribution (regression coefficient B; Wald χ^2; p-value; AIC, n = 194). Environmental variables: water surface area of the river at the transect; total shoreline length; mean and SD of NDVI of water in the Nile; (%) of land cover class (tree, shrub, grassland, cropland, wetland, sparse vegetation, urban area, and deep water) in the surrounding landscape in different buffers (100, 500, 1000, 5000 m); mean and SD of NDVI in the buffer at multi-spatial scale; Shannon–Wiener diversity index H′ for all land cover classes. Scale refers to the best fitting buffer per environmental variable on the basis of the highest absolute correlation coefficient with the dependent variable. The last four columns refer to the output of a logistic binary regression on predicting the probability of reporting red-listed species in the transect. Empty cells indicate non-significant correlations.

	Species richness				Abundance				Evenness				H′				Probability of reporting red-listed species			
	Scale	B	Wald χ^2	p	Scale	B	t	p	Scale	B	t	p	Scale	B	t	p	Scale	B	Wald χ^2	p
Water surface area		<0.001	<0.001	0.001		0.317	4.252	0.001						0.227	3.21	0.002				
Shoreline length	No significate correlation																			
NDVI mean Water		−1.003	22.79	0.001														−3.761	2.816	0.093
NDVI SD Water						−0.346	−4.641	0.001		0.148	2.05	0.042								
Tree									5000	−0.22	−3.06	0.003								
Shrub	5000	−3.263	4.610	0.032													5000	−58.951	6.661	0.010
Grassland	No significant correlation																			
Cropland	No significant correlation																			
Wetland	No significant correlation																			
Sparse vegetation	No correlation																			
Urban area	5000	−0.005	7.026	0.008													5000	−0.0910	4.82	0.028
Deep water																	1000	0.00000007	4.724	0.030
NDVI SD Buffer	5000	−2.957	4.610	0.001									5000	−0.284	−4.003	0.001	5000	−11.502	4.42	0.036
H′ Land cover	No significant correlation																			
R^2 adj (*=AIC)		1190*				0.119				0.046				0.091			%correct:	75.30%		

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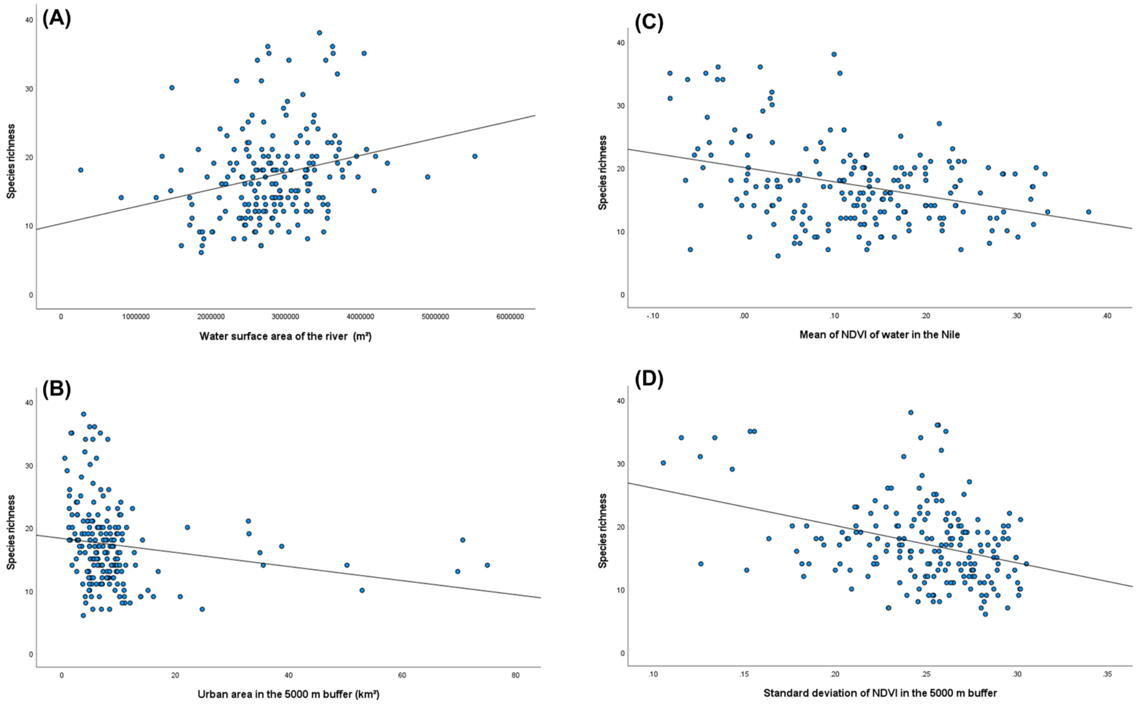

Figure 2. Illustrations of the multiple regression model showing the five significant predictors for the total number of species (y-axis), namely: the water surface area (m^2) in the transect (A), urban area (km^2) in the 5000 m buffer around the transect (B), mean NDVI of water in the Nile (C), and SD of NDVI in the 5000 m buffer (D).

positively associated with mean NDVI of water in the Nile, with deep water in the 100 m buffer and SD of NDVI in the 5000 m buffer and negatively with water surface area of the river. Waders were positively correlated with water surface area of the river and negatively correlated with mean NDVI of water in the Nile and urban area in the 5000 m buffer.

The PCA explained 50.8% of the variation of the guild composition on the first two axes (axis 1 = 28.4%, axis 2 = 22.4%; Fig. 3a). The environmental variables (supplementary variables) accounted for 18.54% (adjusted explained variation is 13.14%). Wetland in the 5000 m buffer had the largest projection on the first axis. The RDA analysis, constrained by only including the two most important anthropogenic variables from the univariate analyses (urban area and cropland, Table 4) showed that the guild composition was significantly, yet minorly, affected by these two variables (4.8%, Pseudo F = 4.8, p = 0.002; Fig. 3b). Herons showed a positive association with cropland, and raptors were positively associated with urban area, while waders and gulls were negatively associated with urban area and cropland (Fig. 3b).

When graphically exploring species-specific patterns, wader species all followed a similar association pattern to each other, while raptor species varied, with common kestrels *Falco tinnunculus* and western marsh harriers *Circus aeruginosus* being more associated with urban area, while black kites *Milvus migrans* were more associated with cropland (Fig. 3c). The variation among heron species was remarkable, with cattle egrets *Bubulcus ibis* following the anthropogenic land cover but grey *Ardea cinerea* and purple herons *Ardea purpurea* negatively correlating with both urban area and cropland. We observed the same pattern in dabbling ducks, where mallards *Anas platyrhynchos* were associated positively with cropland while Egyptian geese *Alopochen aegyptiaca* showed a negative correlation (Fig. 3c).

The probability of detecting red-listed species was affected by multiple environmental variables. Overall, the probability of recording red-listed species decreased with increased urban area (Table 3, Fig. 4). It was also negatively associated with the NDVI of water in the Nile, shrub cover in the 5000 m buffer, and the variation of the NDVI in the 5000 m buffer. The red-listed species showed only a weak positive association with deep water in the 1000 m buffer.

Discussion

With a rising number of anthropogenic pressures on species, it is becoming crucial to obtain a good understanding of the differential effects stressors may have on animal communities. Such knowledge is key for effective conservation measures. Here, we used a large waterbird census (970 km; > 96 000 waterbirds and raptors counted) along the Nile in Egypt with varying degrees of human presence to assess the effect of anthropogenic land cover types (defined here as urban area and cropland) on the waterbird communities at multiple spatial scales.

The strong variation in bird counts along the Nile, ranging from 28 to 10 743 individuals and 6–38 species per 5000 m transect, highlights the variation in suitable habitats along the river and urges to obtain deeper insights at higher spatial

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Table 4. Regression analysis results (standardised regression coefficient B; t-value; p-value; R^2 adjusted, n = 194) to predict the effect of different variables on the relative contribution (%) of each guild in terms of total number of species. Guilds are dabbling ducks and gallinules; diving birds and deep-water feeders; gulls; open water fishing birds; raptors; stalking herons, ibises and storks; and waders. Environmental variables: water surface area of the Nile in a transect; total shoreline length; mean and SD of NDVI of water in the Nile; (%) of land cover class (tree, shrub, grassland, cropland, wetland, sparse vegetation, urban area, and deep water), in the surrounding landscape in different buffers (100, 500, 1000, 5000 m); mean and SD of NDVI in the buffer at multi-spatial scale; Shannon–Wiener diversity index H′ for all land cover classes. Scale refers to the best fitting buffer per environmental variable on the basis of the highest absolute correlation coefficient with the dependent variable. Empty cells indicate non-significant correlations.

	Dabbling ducks and gallinules				Diving birds				Gulls				Open water fishing birds				Raptors				Stalking herons, ibises, storks				Waders			
	Scale	B	t	p	Scale	B	t	p	Scale	B	t	p	Scale	B	t	p	Scale	B	t	p	Scale	B	t	p	Scale	B	t	P
Water surface area						0.225	2.952	0.004														−0.261	−3.836	0.001		0.287	3.758	0.001
Shoreline length																		0.131	1.98	0.049								
NDVI mean Water														−0.243	−3.607	0.001						0.319	4.239	0.001		−0.230	−3.280	0.001
NDVI SD Water						−0.301	−3.939	0.001																				
Tree																	5000				5000							
Shrub																	100	0.279	4.249	0.001	100							
Grassland	100	−0.156	−2.247	0.026													5000				1000							
Cropland	No significant correlation																											
Wetland	5000	−0.239	−3.440	0.001					5000	0.327	4.779	0.001	5000				5000	0.268	4.036	0.001	1000				5000			
Sparse vegetation	No significant correlation																											
Urban area													1000	0.279	4.141	0.001	5000								5000	−0.172	−2.351	0.020
Deep water									5000	−0.195	−2.85	0.005	100								100	0.171	2.587	0.01	1000			
NDVI SD Buffer																	5000	0.177	2.672	0.008	5000	0.161	2.254	0.025				
H′ Land cover	No significant correlation																											
R^2 adj		0.07				0.075				0.117								0.171				0.209				0.143		

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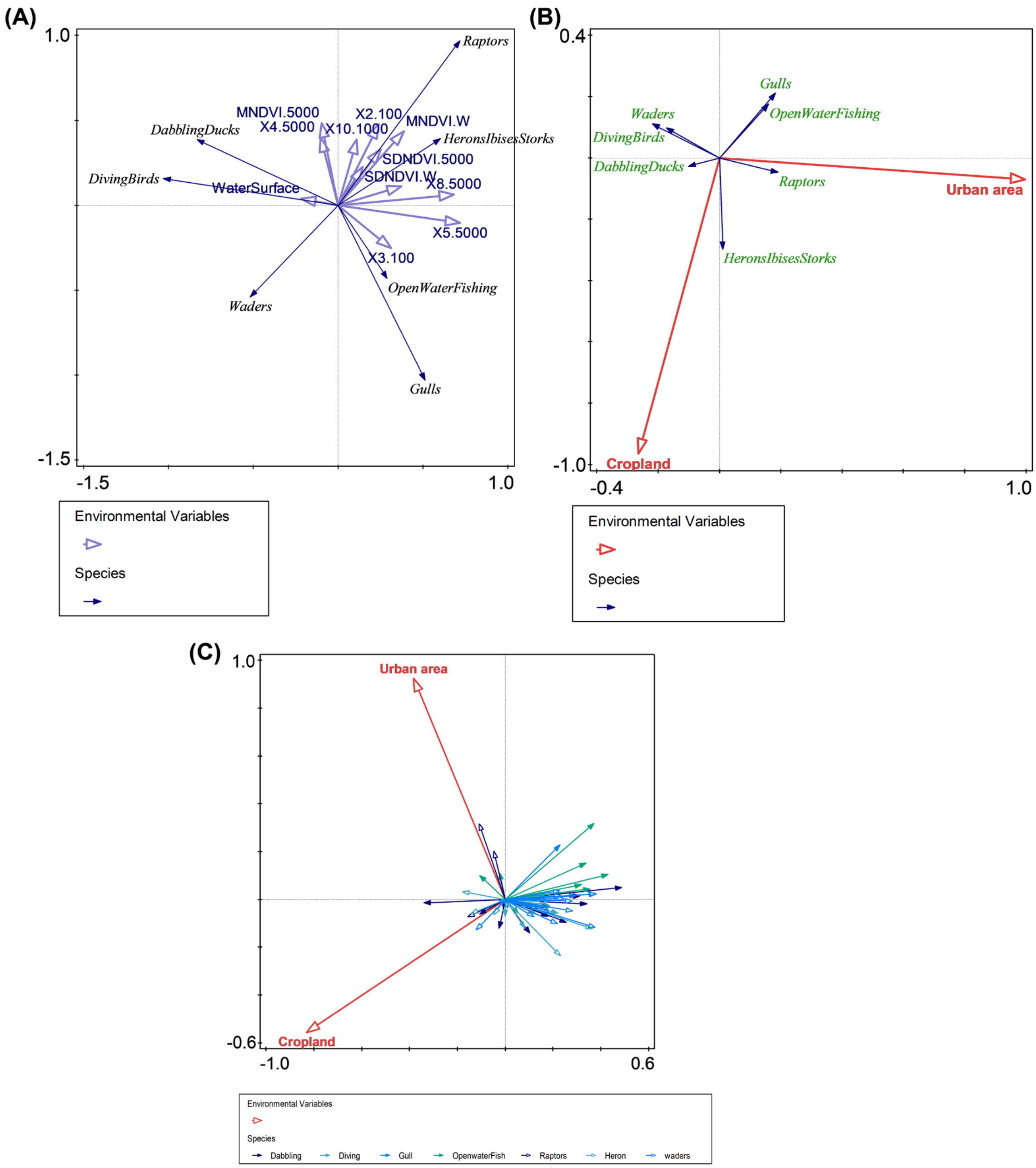

Figure 3. PCA of the guild composition (A), RDA, a constrained analysis, showing the effect of the two anthropogenic land cover, i.e. urban area and cropland in 5000 m buffer on the guild composition (B), and RDA of the species composition coded by guild (C).

resolution into which factors are most limiting and disturbing. Not surprisingly, the transects with the fewest birds were recorded near highly urbanised area, while the transects with the highest bird abundance were in areas with low human impact, a pattern also reported in other studies (Blair 1996, Bellocq et al. 2017). Species richness, abundance and the Shannon-Wiener species diversity index were all positively related to the water surface area of the river within the transect (Paszkowski and Tonn 2000). We further show that the species richness correlated negatively with the presence of anthropogenic land cover (i.e. urban area) and with SD of NDVI (the variation in vegetation cover) at a larger spatial scale (buffer size of 5000 m) (Burton 2007). Furthermore, urban area also had a negative effect on threatened species. Urbanisation induces habitat fragmentation and habitat loss, but also direct disturbance factors may thus affect those sensitive species (Boggie et al. 2018).

Our findings for the guild composition led to a finer picture of which environmental factors are relevant for species with similar ecological niches. As predicted, we show that typical waterbird guilds, such as diving ducks and waders, associated positively with the shoreline length and water

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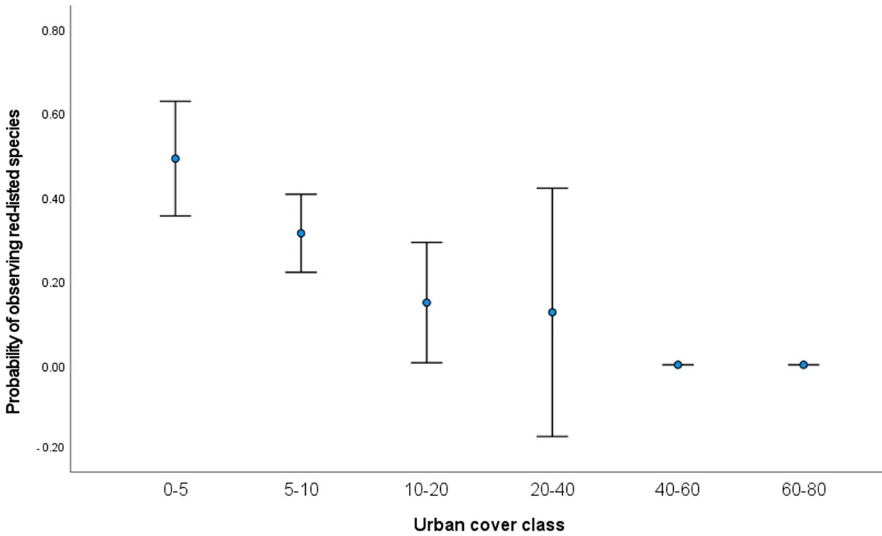

Figure 4. Observed probability (+/− 95% confidence interval) of recording a red-listed species in relation to increasing urban areacover in six classes (from 0–5 to 60–80%).

surface area of the river within the transect, which might provide a safe distance from the direct human disturbance on shore (Paszkowski and Tonn 2000). Raptors associated more with the shoreline, where they can roost and hunt in shallow waters. Moreover, raptors benefited from wetland cover at a larger spatial scale to suit their extensive foraging range (Kumar et al. 2022, Tapia and Zuberogoitia 2018). An unexpected negative association of grassland cover in the 100 m buffer around the Nile and the abundance of dabbling ducks and gallinules might be linked to human impact. Those green patches near the river shorelines attract humans for recreation and other activities, which shows how direct human disturbance can affect the distribution of that guild (Murphy and Romanuk 2014). Wetland cover in the surroundings of the Nile negatively affected the presence of dabbling ducks and gallinules, presuming that those wetlands attract dabbling ducks by providing suitable habitats for the guild compared to the Nile habitats (Murray et al. 2013, Rajpar et al. 2022). Interestingly, urban area did not affect all guilds as we expected. In contrast to our predictions, urban area positively correlated with the presence of open-water fishing birds. One reason may be the expansion of fishing activities in urban area, which often attracts those birds to feed on leftover fish (Manosa et al. 2004). Mean NDVI of water in the Nile, which indicates water clarity, was negatively associated with open-water fishing birds. The species in this guild need good visibility to find fish (Ghim and Hodos 2006, Strod et al. 2008). The general negative effect of urban area on waders is not surprising, as waders rely on mudflats, yet urban infrastructure and buildings degrade or replace such suitable shores (Kang et al. 2015, Xu et al. 2022). Moreover, herons, dabbling ducks and raptors did not show a positive relation to urban areas, as we had predicted. We assumed that they would benefit from human presence by foraging on garbage or crops (Chace and Walsh 2006). However, there clearly is another factor that obscures this possible positive effect of urban area, such as direct human disturbance. The guild approach has been used successfully to obtain a holistic view of bird community composition (O'Connell et al. 2000, Karp et al. 2011, Marja et al. 2013), and it can give indications of habitat quality (O'Connell et al. 2000, Bryce et al. 2002). However, guild-level analysis did not explain the general requirements of birds in our dataset. While birds of the same guild generally share the same habitats and food resources, they do not necessarily have the same specific requirements, as one guild can contain both generalist and specialist species (O'Connell et al. 1998). Moreover, species within the same guild can react differently to specific environmental variables or human disturbance levels (Tratalos et al. 2021). To gain better understanding of how species react to different environmental variables, more fine scaled data at species level are needed as well as taking the direct human disturbance in consideration e.g. the number of people present, and the presence of boats (Murphy and Romanuk 2014).

Our study site provides a unique opportunity to study bird communities over such a long stretch of wetland habitat of global importance. The Nile, since long an environment for resident and migratory birds and humans in an arid zone, provided a case study to identify habitat requirements for birds in a clearly defined human-induced landscape. The more than 96 000 birds we counted are just a fraction of the resident and migratory birds relying on these habitats as wintering grounds or stopover sites, and yet we show how important not only the Nile itself is but also the surrounding landscape. The human population in Egypt was estimated to be 113 million in 2023, with 90% living close to the Nile (about 5% of the country area) and 41% inhabiting urban areas (Worldmeter 2023). With the water scarcity in the country, most of the urban expansion is taking place along the Nile, producing strong pressures on natural resources such as water, soil, natural vegetation and biodiversity, which are expected to continue to increase giving the growth rate

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of human population (Seto et al. 2012, Bonnet-Lebrun et al. 2021, Worldmeter 2023).

The importance of the spatial context in assessments of impacts on species distributions and abundances (Borges et al. 2017) is emphasised by our study. Not only were species richness and the occurrence of rare species negatively affected by the anthropogenic land cover in the 5000 m buffer around a transect, also many guilds were best predicted by the presence of habitat classes in the 5000 m buffer around the transect rather than that in the other buffers. These findings all show how important the wider environment is for predicting the relative abundances of species (Westphal et al. 2003, Schindler et al. 2013, Hamza and Selmi 2018).

Our findings thus show how important environmental factors are for community composition within a wider landscape. This has strong implications for conservation, since very local efforts might not be sufficient when species presence relies on a wider area (Beatty et al. 2014). Such larger areas may be used as foraging grounds for resident birds and attract migratory birds, supplying suitable wintering ground or stopover sites, even if they make use of only a small proportion of this wider landscape (Borges et al. 2017). Our results show that specifically, the wider surrounding appeared most relevant in predicting waterbird presence in this environment. This highlights the importance for finding solutions of optimised co-existence of humans and wildlife in this area, i.e. a convivial conservation approach, with implications to similar areas of conflicts elsewhere (Büscher and Fletcher 2019, Massarella et al. 2022). Future studies clearly need to identify the more detailed disturbance factors, separated by stationary structures such as urbanisation and agriculture, from activity-based disturbances by humans, such as from fishermen, or boat traffic, which could act on a much more local scale.

Acknowledgements – We would like to thank Khaled Noby, Mohamed Ezat, Amr Hady, Hosny Asran and Ahmed Ebaid for helping in data collection, and Ayman Hamada, Khaled Allam, Pierre Defos Du Rau and Jean-Yves Mondain-Monval for facilitating the fieldwork.

Funding – Field work was a part of International Waterbird Census, IWC 2017/2018 in Egypt funded by the RESSOURCE project with support and facilitation by the Egyptian Environmental Affairs Agency, L'Office français de la biodiversité (OFB) and Tour du Valat. The INREF ECO2 project at Wageningen University and Research funded the project. The first author (HM) was supported by grants from the A. G. Leventis Foundation and the Lucie Burgers Foundation.

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Haitham Mossad: Conceptualization (lead); Data curation (lead); Formal analysis (equal); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (equal); Resources (supporting); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (lead). **Anouschka R. Hof**: Conceptualization (supporting); Supervision (equal); Validation (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Lysanne Snijders**: Formal analysis (supporting); Supervision (equal); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Marc Naguib**: Conceptualization (lead); Funding acquisition (lead); Investigation (supporting); Project administration (lead); Resources (lead); Supervision (lead); Validation (equal); Writing – original draft (lead); Writing – review and editing (lead). **Willem Frederik de Boer**: Conceptualization (lead); Data curation (supporting); Formal analysis (lead); Funding acquisition (lead); Investigation (supporting); Methodology (lead); Supervision (lead); Validation (lead); Visualization (lead); Writing – original draft (equal); Writing – review and editing (lead).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.280gb5mzz (Mossad et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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