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Diversity and Distribution of Waterbirds across Wetlands of Eastern Uganda

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Authors' contributions

This work was carried out in collaboration with all the authors. Authors NS and PMM designed the Study and collected data. Authors NS and FT performed the statistical analysis and wrote the first draft of the manuscript. Author PMM gave comments. All authors read and approved the final manuscript.

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ABSTRACT

Explaining patterns of diversity, and abundance across sites is a central aim of community ecology. Avian communities have been the focus of many studies on species diversity. To be able to explain patterns of waterbirds in wetlands of eastern Uganda, we conducted a rapid assessment in 48 wetlands (38 swamps, two rice paddies and eight lakes) using total counts. We examined waterbird assemblages in these wetlands in relation to wetland area, wetland type, water depth, water pH and the time of year/season. Statistical analysis were conducted using Genstat Version 8.1 (VSN Intl.2003, in which General Linear Mixed Models were used to examine the variations. In total, 9,410 birds from 64 species and 17 families were recorded. Species diversity and overall abundance varied significantly among wetland types and between seasons. Rice paddies were both more species-diverse than lakes and swamps. Wetland area had significant independent and positive effects on the waterbird community. In addition to explaining differences among wetland types in waterbird numbers, water depth had a positive effect on some aspects of the waterbird community with no significant effect of pH. These results imply that an interplay of factors is responsible for the pattern and structure of waterbird communities on wetlands in eastern Uganda.

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Keywords: Diversity; waterbirds; wetland type; statistical analysis; Eastern Uganda.

1. INTRODUCTION

Wetland ecosystems have some of the highest levels of biodiversity and productivity in the world [1]. However, these habitats are affected as human populations expand [2], primarily through draining for agriculture [3]. Waterbirds, particularly wading birds, have been used as indicators of the quality of habitats [4-6], and because of this, there is a need to collect data on the status of avian populations in Ugandan wetlands. Such data can then be used to make informed management decisions on species and habitat protection [7,8]. The most fundamental description of a community is provided by a measure of its diversity, which is based on species equitability (or heterogeneity) i.e. the number of species of organisms or species richness [9], and their abundance [10], which are in turn controlled by physical environmental variables and other species present [11]. Species richness and abundance are usually closely related and, have been used to calculate diversity indices that are considered one of the most important attributes when assessing the wildlife conservation value of a site [12]. In most studies [13-15], including this one, count data are used as an estimate of species diversity.

Communities of organisms have been observed to vary along a number of ecological environmental variables i.e. the size of the habitat [16]. The species –area relationship is thought to be based primarily on a positive correlation between habitat heterogeneity and or/population size and area [16] and as such the strength of the species-area relationship in various ecosystems or community types has been used as a foundation for much land-ecosystem conservation planning.

In addition to area of the habitat, other factors such as water depth, water quality, seasonal fluctuations and habitat types and productivity [17,18] have been found to predict the number of birds in a habitat. For example waterbird distribution at any given time of year mirrors closely the availability of water and the resulting productivity of ephemeral and permanent wetlands. Water depth has been shown to have effects on waterbird abundance and distribution, with high water levels often detrimental for some species as drought is for others because they reduce availability of prey [19]. Some of these environmental factors affecting community structure may remain fairly stable over time, such as wetland size, while others may change such as water depth and aquatic vegetation cover.

One of the central aims of avian ecology and conservation biology is therefore to understand which factors determine different numbers of species in different habitats or regions. This study, therefore, applies a community ecology approach to assess the relationships between waterbird species diversity and abundance and environmental parameters in a cross section of wetlands in eastern Uganda. We hypothesized that the diversity and abundance of waterbirds on a wetland would be higher on bigger than smaller wetlands, and that habitat characteristics such as water depth and the amount of aquatic vegetation would vary between wetland types and between seasons, and this variation would have different effects on the waterbird diversity, abundance and distribution. For the purpose of this study, waterbirds have defined as birds that are ecologically dependent on aquatic environments. This includes the species of waterfowl as defined by [20] and wetland birds of prey and kingfishers that are classified as wetland birds. In Uganda they include, but are not restricted to, 26 families, 17 of which were detected in this study.

2. STUDY SITES

The Wetlands Inspection Division (WID), working under the National Wetlands Programme (NWP) has mapped and documented all wetlands in Uganda using Geographic Information System (GIS) technology, a list from which our study sites were selected. This study was conducted in five districts of eastern Uganda, namely Mbale, Tororo Pallisa, Bugiri and Kumi. A total of 48 wetlands were visited, two of which were commercial paddy rice growing areas, with a total area 19 km^2, eight lakes with a total area of 287 km^2 and 38 swamps with an area of 586 km^2 (See Fig. 1). Taken together, 32 sites/wetlands (67%) of my study sites fall into the category of seasonal wetlands, while 16 (33%), permanent wetlands. Most of the wetlands are located in very remote places with poor road networks. This prevented complete randomization in selecting the study sites, so the 48 sites represent a non-random sample, i.e. choice of wetlands was biased by closeness to roads. However, I selected wetlands representing all the types found in the three districts. Sites were visited twice, first in July-August 2018, and then January-February 2019.

2.1 Study Methods

2.1.1 Waterbird survey

Birds were counted along a 5 km line transect [21]. The line transects were approximately 300 m wide (150 m on each side), and those in wetlands <5 km in length were not in straight lines. All waterbirds seen along this transect were counted and recorded. To avoid having biased estimates, we surveyed each wetland twice, once in July-August 2018 and again in January-February 2019, which are the two dry seasons in a year. All observations were made during

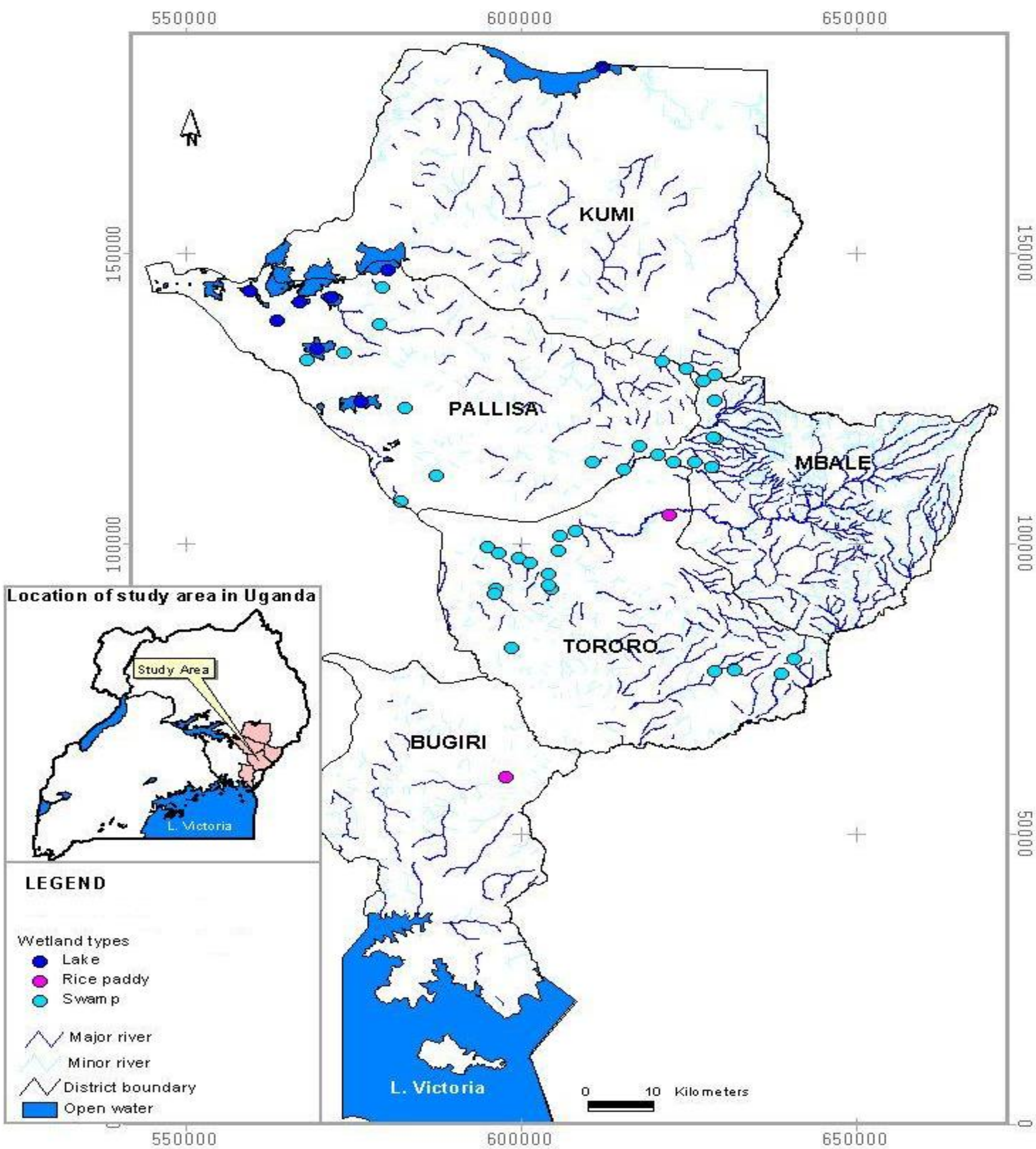

Fig. 1. Study area in eastern Uganda and spatial distribution of the 48 selected wetlands

daylight hours (0730-1600) using a 22 x-spotting telescope and 8 x 40 binoculars. All birds seen were counted and recorded. Counts were not done on days of extreme weather e.g. very strong winds. For lakes, counts of birds were done at the shoreline. This was carried out from a boat at distances varying from 150-200 m from the shoreline depending on the water depth. For all the seasonal, and some permanent swamps counts were done on foot. Most surveys lasted 1-5 hours depending on the number of birds present. Advantage was taken of termite mounds and raised points that are characteristic of most swamps in Uganda.

Our study sites included lakes, swamps and rice paddies, all of which varied in their vegetation structure. Detectability of small secretive species and/or camouflaged ones such as Malachite Kingfisher *Alcedo cristata* may have varied among these three wetland types. The abundance estimates of such birds may have underestimated their population. However, the larger and more conspicuous species such as Grey Heron, Black-headed Heron were almost certainly not affected since the vegetation in these wetland types was relatively short. The number of birds recorded has been observed to vary with time of day, with more birds recorded shortly after dawn and before dusk [21]. During my study most bird counts lasted about 5 hours, i.e. from 0730-1230. Bird counts were started late (from 1100-1600) at only two sites due to delays in acquiring a boat. Considering that there were 48 sites, abundance estimates from these two sites did not have a major effect on the final results.

2.1.2 Environmental variables

A number of environmental variables affect waterbird species diversity and abundance in a habitat. This study collected data on water variables such as depth and pH and habitat characteristics such as area in km^2.

2.1.3 Water depth and pH

Data on water depth and pH, was collected from four different points in the wetland and the average taken as the value for the wetland. Water depth was measured using a marked stick that was dipped into the water, while water pH was taken using standard laboratory pH strips and colour changes were matched on a colour chart.

2.1.4 Wetland area

Coordinates were taken at each site using a Garmin 12 GPS. These were then saved in MSExcel as a dbase IV file, which was then imported in to a GIS program (ArcView 3.1-Applegate 1999). The above GPS readings were overlaid on other already mapped themes such as administrative boundaries, wetlands, roads and rivers. Most wetlands had names and these could be easily identified. In situations where the name was not indicated in the wetlands map, the GPS names were used. The area of each site was determined by drawing polygons around the wetland boundaries.

2.2 Data Analyses

2.2.1 Diversity indices, and waterbird abundance

Shannon-weaver indices (H') of species diversity were calculated for each count. This index is based on the relative composition of species in an area and how equally the individuals are distributed among the species groups or taxa. The more equal the distribution, the greater the overall diversity [22]. Overall waterbird abundance was taken as the total number of individuals in each count.

The Shannon-weaver diversity index, H' was calculated for each count as:

$$H' = -\sum(\text{Total of bird species})/(\text{Total birds}) \times (\ln(\text{Total of bird species})/(\text{Total birds}))$$

Waterbirds were also classified into migrants and resident birds to establish if wetlands in eastern Uganda are used as stopover habitats for migrating birds, and if these birds were randomly distributed among wetlands. Migrant birds consisted of Palearctics, afro-tropical migrant and species with at least some palearctic populations while the residents were birds that are known to stay in Uganda throughout the year.

2.2.2 Model selection

Shannon diversity and Overall waterbird abundance were used as response/dependent variables and; year/season, Wetland area, Wetland type, water pH and water depth as explanatory/independent variables. Data for only 40 wetlands were included in the analyses involving Shannon diversity and eight wetlands were excluded because no birds were found using these wetlands during the January-February season of 2019. These sites were excluded because this index gives sites for which there were no birds recorded a similar index with those sites for which one species of bird was recorded with say 100 individuals. Because the analyses involved more than one explanatory variable, multiple regressions were used. One-sample Kolmogrorov-Smirnov test was done to examine whether the dependent variables were normally distributed. Data that did not conform to the normal distribution were natural log-transformed after adding one (ln(x+1) to reduce skewness and kurtosis (homogeneous variance).

Generalised Linear Mixed Model (GLMM) in Genstat version 8.1(VSN Intl.2003) were done in which all independent variables where included without elimination. The Wald statistics/degrees of freedom was tested against the χ^2 distribution and effects were considered significant at P≤0.05. Considering that data were collected during two different years (seasons), we included year as a fixed effect in the model. Since each wetland had two data points, I controlled for pseudo-replication [23] by considering individual wetlands (site) as a random effect.

2.3 Wetland Type Characteristics

Average wetland area was 18.6 ± 3.9 km^2 (range 0.69 to 207 km^2) and this varied significantly among wetland types (P <0.001), with a mean of 9.5 ± 0.5 km^2 for rice paddies, 35.9 ± 11.1 km^2 for lakes and 15.4 ± 4.3 km^2 for swamps (Table 2). Water depth varied significantly among the wetland types, and water depth of all wetlands ranged from 0 cm (swamps) to 350 cm (lakes), with a mean of 57.5 ± 10.4 cm (Table 2). The mean water depth on all wetlands during the July-August 2018 season was significantly different from that of January-February 2019 (P<0.001). Other water quality parameters for example turbidity and amounts of nitrates also varied among wetland types but not between seasons (P>0.05). No significant variations were observed in water pH.

2.3.1 Waterbird community description

A total of 9,410 birds from 64 species and 17 families were recorded, with Families Anatidae and Ardeidae comprising the most abundant comprising together 54% of the total (see appendix i). Waterbird diversity ranged from 0 to 2.85 species, with an overall mean of 1.63 ± 0.08 species while the average overall abundance was 98.0 ± 24.1 individuals (range: 0 to 1713 individuals) (Table 3). Almost 80% of the waterbirds were residents with a small proportion of migrant species. Some individual species occurred at only one (2.08%) wetland (e.g. Black Egret- *Egretta ardesiaca*), while others occurred at all the 48 (100%) wetlands (e.g. Cattle Egret - *Bubulcus ibis*). (see appendix i).

2.3.2 Bird, environmental and habitat relationships

One-sample Kolmogrorov-Smirnov tests showed that only species diversity conformed, to the normal distribution and species abundance did not, even after log transformation (Table 4). It is evident from Multivariate analyses that environmental and habitat variables had different influences on the waterbird community. For example, the size of a wetland had a significant effect on species diversity (Table 5: GLMM: χ^2 = 15.4, df = 1, P<0.001). However, the overall abundance of waterbirds was independent of the size of wetland (Table 6: GLMM: P>0.05). Species diversity increased with increasing size of a wetland.

Table 1. Explanatory variables included in statistical models of waterbird diversity and abundance

Variable	Description
Year/Season	The study period (July-August 2018 and January-February 2019)
Wetland area (sq. km)	Total area of a wetland determined from GIS data using Arc view version 3.1
Wetland type	Whether a lake, rice paddy or a swamp.
Water pH	Acidity/alkalinity of water levels
Water depth (cm)	The average water levels in a wetland.

Table 2. Summary of the habitat variables in all wetlands (lakes, swamps and rice paddies)

Explanatory variable	Wetland types				*Statistics		
	All wetlands (n = 48)	Rice paddies (n = 2)	Swamps (n = 38)	Swamps (n = 38)			
	Mean ± SE (min-max)	Mean ± SE (min-max)	Mean ± SE (min-max)	Mean ± SE (min-max)	χ^2	df	P-value
Area (km^2)	18.6 ± 3.9 (0.69-207)	9.5 ± 0.5 (8.6 – 10.4)	35.9 ± 11.0 (6.7 – 130)	15.4 ± 4.3 (0.69 – 207)	295.7	2	<0.001
Water depth (cm)	57.5 ± 10.4 (0 – 350)	18.9 ± 5.4 (7.9 – 33.4)	258.3 ± 10.4 (200 – 350)	17.3 ± 5.6 (0 – 250)	6965.5	2	<0.001
Water pH	7.2 ± 0.1 (6 – 8.8)	7.8 ± 0.34 (7.7 – 8.8)	7.1 ± 0.11 (6.3 – 7.8)	7.1 ± 0.1 (6 – 7.5)	0.22	2	0.896

**P-values to show how each of the explanatory variables differs among wetlands types*

Table 3. Summary of the waterbird community in all wetlands, and in the 3 different wetland types

Variable	Wetland types			
	All wetlands (n = 48)	Rice paddies (n = 2)	Lakes (n = 8)	Swamps (n = 38)
	Mean ± SE (min-max)	Mean ± SE (min-max)	Mean ± SE (min-max)	Mean ± SE (min-max)
*Species diversity (H')	1.63 ± 0.08 (0 - 2.85)	2.51 ± 0.16 (2.16 – 2.85)	2.28 ± 0.07 (1.88 – 2.67)	1.39 ± 0.09 (0 – 2.81)
Overall waterbird abundance	98.0 ± 24.1 (0 - 1713)	1110.3 ± 203.9 (813 – 1713)	119.6 ± 19.9 (35 – 291)	40.2 ± 8.0 (0 – 425.0)

**n = 40, eight sites were excluded from the calculation of the Shannon index of diversity because no birds were found using the wetland during the January-February 2019 season*

2.3.3 Spatial and temporal variation

Simple linear regression showed significant effects of the explanatory variables on the response variable except for water pH (Table 5). Species diversity varied significantly among wetland types (Table 6: GLMM: χ^2 = 17.71, df = 1, *P*<0.001), with similar results obtained for overall abundance (Table 7: GLMM: χ^2 = 6.33, df = 1, *P* = 0.042). Rice fields were more species rich and diverse than lakes and swamps, but were more similar to lakes than swamps. Similarly, rice paddies supported a higher abundance of waterbirds than lakes and swamps (Fig. 2). Species diversity also varied significantly between the two seasons (Table 5), with a higher diversity recorded in July-August 2018 than in January-February 2019 (Fig. 3).

2.3.4 Relationship with water depth and water pH

Water depth varied among wetland types and the simple liner regression shows a significant effect of water depth on waterbird diversity and abundance (Table 2). However, the multiple linear regression shows a non-significant effect of water depth on waterbird numbers. This observation was also the case with water pH.

2.3.5 Migrants and resident birds

The waterbird community comprised more resident than migrant waterbirds, and the abundance and number of species of both residents and migrants varied among wetland types, with higher numbers recorded on rice paddies than lakes and swamps (Table 8 and Fig. 4). Seasonal variations were also observed in the abundance and number of species of resident and migrating birds, with higher numbers recorded in July-August 2018. A further look into migrating birds shows that Afrotropical migrants contributed the bulk of the migrants in July-August 2018, while the Palearctic migrants were the most abundant and species rich in the January- February 2019 season (Table 8).

Table 4. One-sample Kolmogorov-Smirnov test examining all the response variables for normal distribution

Variables	Untransformed data			Natural log transformed data		
	Z-score	*P*-value	n	Z-score	*P*-value	n
Species diversity (H’)	0.895	0.399	40	na	na	na
Overall waterbird abundance	2.312	<0.001	48	0.540	0.932	48

Analysis was done using the mean values for the two seasons, and 1 was added to all variables before log transformation to account for zeros i.e. In (x+1), n = sample size, na = not applicable

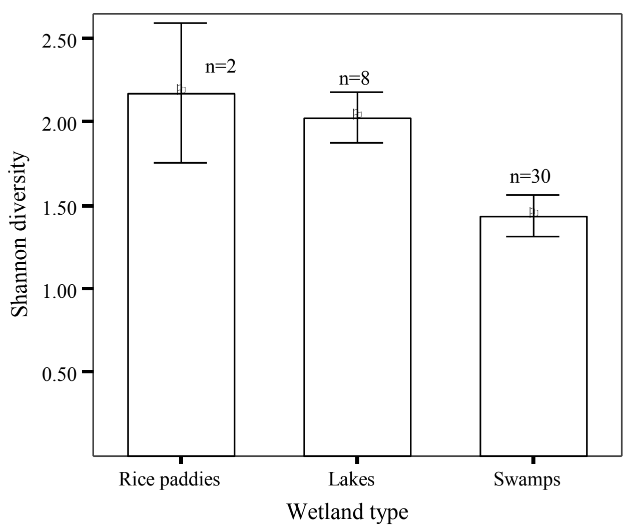

Fig. 2. Species diversity (mean ± SE) in the different wetland types. Sample sizes are given above each bar

Table 5. Generalized linear mixed models of species diversity and overall abundance with each of the explanatory variables

Explanatory variables	**Response variables**					
	Species diversity (H')			**Log species abundance (N)**		
	Coefficient ± SE	χ^2	***P*-value**	**Coefficient ± SE**	χ^2	***P*-value**
Season	A. 0	9.02	0.003	A. 0	7.83	0.005
	B. -0.48 ± 0.16			B. -0.96 ± 0.34		
Wetland area	0.006 ± 0.002	8.99	0.003	0.01 ± 0.004	9.82	0.002
Wetland type	A. 0		<0.001	A. 0		<0.001
	B. -0.22 ± 0.09	31.29		B. -2.35 ± 0.43	56.93	
	C. -0.12 ± 0.09			C. -4.33 ± 0.43		
Water pH	0.18 ± 0.13	1.84	0.175	0.94 ± 0.32	8.53	0.003
Water depth	0.004 ± 0.0007	25.4	<0.001	0.007 ± 0.002	17.4	<0.001

Wetland types: A = Rice paddies, B = Lakes and C = Swamps, and Season: A = July-August 2018, and B = January-February 2019

Table 6. Generalized linear mixed model of species diversity (H'). Eight sites have been excluded from this analysis (n=40)

Variables in model	Coefficient ±SE	χ^2	df	*P*-value	R^2
Season	A. 0	14.25	1	<0.001	45.6
	B. -0.47 ± 0.13				
Wetland area	0.01 ± 0.002	15.40	1	<0.001	
Wetland type	A. 0				
	B. -0.71 ± 0.15				
	C. -1.16 ± 0.15	17.71	2	<0.001	
Water depth	0.001 ± 0.002	0.80	1	0.371	

Table 7. Generalized linear mixed model of log abundance (N)

Variables in model	Coefficient ±SE	χ^2	df	*P*-value	R^2
Season	A. 0	1.45	1	0.455	20.5
	B. -0.47 ± 0.13				
Wetland area	0.01 ± 0.002	15.40	1	<0.432	
Wetland type	A. 0	6.33	2	0.042	
	B. -2.15 ± 0.77				
	C. -1.71 ± 0.77				
Water depth	-0.013 ± 0.029	2.51	1	0.662	

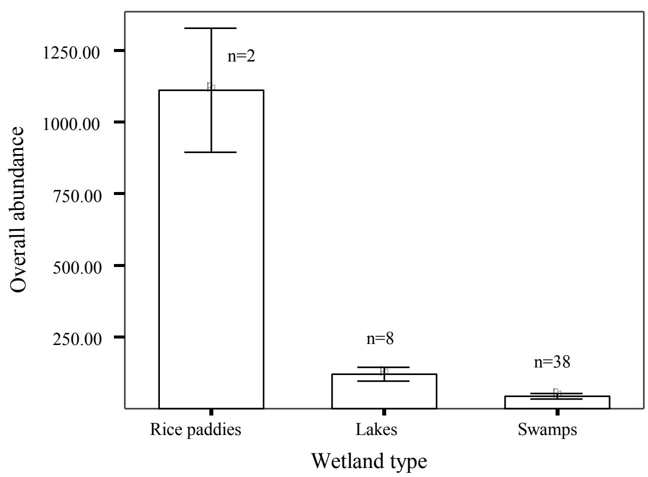

Fig. 3. Overall abundance of waterbirds (mean ± SE) in the different wetland types. Sample sizes are given above each bar

Table 8. Seasonal variation in the abundance and number of species of migrants and resident waterbirds in each wetland type

	July-August 2018						January- February 2019					
	Rice paddies		Lakes		Swamps		Rice paddies		Lakes		Swamps	
Migration status	S	N	S	N	S	N	S	N	S	N	S	N
Afro tropical migrants (A)	2	413	1	26	2	277	1	170	1	18	2	36
*With some Palearctic populations (p)	1	1	1	1	2	73	2	242	2	5	1	80
Palearctic migrants (P)	4	112	3	31	3	102	14	360	4	65	5	247
Residents (r)	28	1389	22	665	29	1779	27	1794	29	1103	20	461

*S = number of species; N = total individuals; *Some individuals are Palearctic migrants*

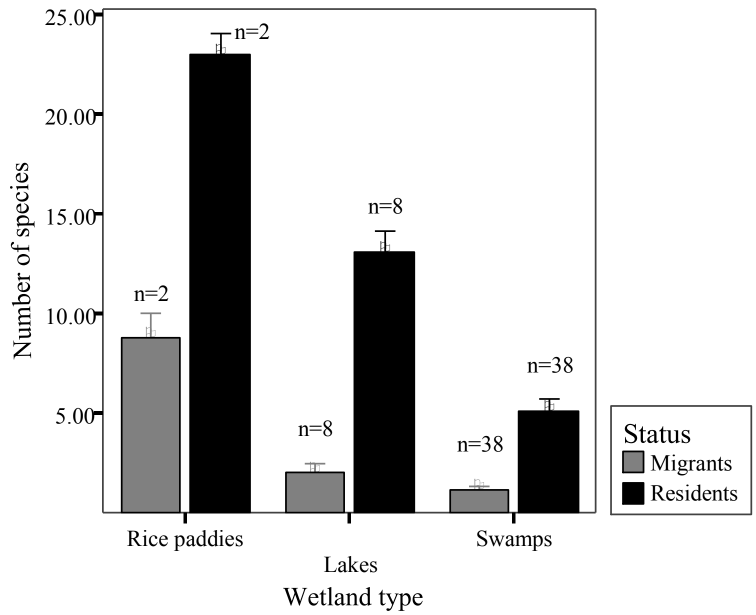

Fig. 4. Number of species of migrant and resident waterbirds (mean ± SE) in the different wetland types

3. DISCUSSIONS

Organisms are not uniformly dispersed in their environment mainly because the environment is never completely homogeneous. The results of the community analyses illustrate several ecological factors, which contribute to species diversity and abundance, and thus the spatial patterns of waterbirds on wetland ecosystems in eastern Uganda.

3.1 Waterbirds and Wetland Area

We found significant positive relationships between the size of a wetland and the waterbird community. These results confirm the importance of habitat size in explaining avian diversity in wetlands, which is consistent with results of other studies in a variety of environments [11,12]. Because habitat heterogeneity usually increases with wetland area, it might explain part of the results [17]. Larger wetlands may be able to provide more foraging opportunities and microhabitats to support a greater diversity of waterbirds. Another explanation from this study can be that bigger areas were also deeper (or had water) than small ones, and the majority of the bigger wetlands in this study were permanent, capable of holding water throughout the year, which is important from a conservation perspective.

3.2 Waterbirds and Water Depth and Water pH

The significant relationship between water depth and waterbirds indicates its importance to waterbirds. For example, the absence of water on a wetland has been observed to cause changes in avian community structure through changes in food resources [24]. Currently, the use of chemicals in Uganda's agricultural systems is at a very low level in the rural areas. Impairment of water quality from industrial and agricultural effluents is not a national issue at present. This may partly explain the non-significant results obtained between waterbird diversity and water pH. Although there is very little indication of pollution in the wetlands of eastern Uganda, at the moment, the potential problems deserve some attention otherwise degradation of these ecosystems could go unnoticed for a long time and eventually bring disastrous effects.

3.3 Spatial Variations

Species diversity and overall abundance varied among wetland types, with higher numbers recorded on rice paddies than lakes and swamps. Rice fields are reasonably shallow wetlands, and these have been observed to support a greater number of waterbirds than deeper wetlands [25]. This is because they offer a mixture of mud and open water of variable depth where as deep wetlands offer only flooded habitats. In addition, shallow waters have been observed to concentrate prey [8]. And since the bulk of the populations of birds recorded in this study were waders, which have a preference for shallow waters for foraging, rice paddies seem to have provided the most suitable foraging habitat.

Furthermore, these artificial ecosystems (rice paddies) are richer in wildlife partly because farming practices mimic moderately intensive natural disturbance, which is likely to create species-rich communities, although rice fields are unique in their similarity to natural wetlands [25]. The rice growing practice also creates a hemi-marsh (interspersion of open water and vegetation), typical of some of the wetlands in North America that are managed for migrating waterfowl [26]. This type of habitat has been found to provide a diversity of food for waterbirds [27]. In contrast, there is little ecological diversity in uniform stands of papyrus found on most swamps in eastern Uganda. Also in the early stages, the rice crop is short and the fields are sparse. However it is likely that birds were responding to other variables not included in the analysis, for example prey abundance, vegetation cover among others.

3.4 Temporal Variations

Seasonal variations were observed in some aspects of the waterbird community. Higher numbers were recorded during the July-August 2018 season than the January-February 2019. Data for this study was collected in what is considered the dry months of the year in Uganda. The higher waterbird numbers in the July-August season could be as a result of the distorted weather patterns nowadays resulting from global climatic changes. Species diversity has also been shown to be positively correlated with the permanence of the wetland [28] and the suitability of a wetland as a water-bird habitat will depend on the presence of water, which has an effect on soil permeability. The reduced rainfall during the dry season leads to a recession of surface waters, which is contracted to the deeper and permanent wetlands.

3.5 Resident and Migratory Waterbirds

Spatial and temporal variations were also observed between migrant and resident waterbirds. There was a higher abundance of migrant birds on rice paddies than lakes and swamps. In addition, more migrant birds were recorded during the January-February 2018 season than the July-August 2019. On an international level, January and February fall in the mid-winter of the northern hemisphere, a period when many migratory birds concentrate on discrete wetlands in Uganda, and some other countries in Africa [29]. On a regional scale, and possibly on a continental scale too, this is the driest period in a year, when most seasonal wetlands are dry. This may partly explain why rice paddies, which have water almost throughout the year, have the highest concentration of migrant birds. Similarly [29] compared rice fields and natural wetlands (grass and papyrus swamps) at Doho, and found that rice fields were generally more species rich and diverse than the surrounding wetlands, and that these supported a higher number of migrating birds than the natural wetlands. This could possibly be attributed to the fact that the majority of lakes in eastern Uganda are covered by vast amounts of aquatic vegetation and thus are less attractive to migrating birds, since they mainly use stop-over wetlands for foraging.

4. CONCLUSION

Diversity indices reflect some of the complex properties of the structure and dynamics of a complex system. However, most of the available indices have interpretation pitfalls that reduce their overall utility. Nevertheless they are valuable in summarizing information and easing interpretation. Results from our study show that there was a non-random distribution of waterbirds, and that rice agriculture is very important for waterbirds in Uganda, especially during extremely dry times of the year when most seasonal wetlands are dry. Therefore, improved management of rice paddies for aquatic birds may provide a partial solution to the loss of natural wetland habitats in Uganda and possibly in the region. With some birds having a migratory status, the preservation of suitable habitat for them should be of broad concern. Therefore every effort should be made to keep this important farming system compatible with wildlife. However, our results should also be treated with caution because of a small sample size (Two rice growing sites), and that part of the unexplained variance may be attributed to food (prey) abundance and vegetation cover that were not included in these analyses.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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Appendix i: Waterbird assemblage of 48 wetlands in eastern Uganda

Briton no.	Species common name	Scientific name	Family	Freq[1]	Abund[2]	%Freq[3]	%Abund[4]	Status[5]
12	Pink-backed Pelican	*Pelicanus carbo*	Pelicanidae	9	35	18.75	0.37	W
17	Long-tailed Cormorant	*Phalacrocorax africanus*	Phalacrocoracidae	10	80	20.83	0.85	W
18	Greater Cormorant	*Phalacrocorax carbo*	Phalacrocoracidae	2	4	4.17	0.04	W
19	[v]African Darter	*Anhinga rufa*	Anhingidae	1	1	2.08	0.01	W
23	Little Bittern	*Ixobrychus minutus*	Ardeidae	1	1	2.08	0.01	pW
25	[nt]Grey Heron	*Ardea Cinerea*	Ardeidae	19	109	39.58	1.16	W
26	[nt]Goliath Heron	*Ardea goliath*	Ardeidae	5	7	10.42	0.07	W
27	Black-headed Heron	*Ardea melanocephala*	Ardeidae	44	520	91.67	5.53	w
28	[nt]Purple Heron	*Ardea purpurea*	Ardeidae	24	139	50	1.48	W
30	Squacco Heron	*Ardeola ralloides*	Ardeidae	22	454	45.83	4.82	W
32	Cattle Egret	*Bubulcus ibis*	Ardeidae	48	1342	100	14.26	n
34	Great-white Egret	*Egreta alba*	Ardeidae	8	48	16.67	0.51	W
35	[nt]Black Egret	*Egretta ardesiaca*	Rallidae	1	4	2.08	0.04	W
36	Little Egret	*Egretta garzetta*	Ardeidae	28	605	58.33	6.43	W
38	Yellow-billed Egret	*Egretta intermedia*	Ardeidae	7	58	14.58	0.62	W
42	Hamerkop	*Scopus umbretta*	Scopidae	14	27	29.17	0.29	n
43	African Open-billed Stork	*Anastomus lamelligerus*	Ciconiidae	29	863	60.42	9.17	Aw
45	White Stork	*Ciconia ciconia*	Ciconiidae	1	1	2.08	0.01	P
46	[nt]Woolly-necked Stork	*Ciconia episcopus*	Ciconiidae	1	12	2.08	0.13	W
48	[v]Saddle-billed Stork	*Ephippiorhynchus senegalensis*	Ciconiidae	1	1	2.08	0.01	W
49	Marabou Stork	*Leptoptilos crumeniferus*	Ciconiidae	5	11	10.42	0.12	w
50	Yellow-billed Stork	*Mycteria ibis*	Ciconiidae	15	119	31.25	1.26	W
51	Hadada Ibis	*Bostrychia hagedash*	Threskiornithidae	17	194	35.42	2.06	w
53	Glossy Ibis	*Plegadis falcinellus*	Threskiornithidae	9	68	18.75	0.72	pW
54	Sacred Ibis	*Threskiornis aethiopicus*	Threskiornithidae	17	188	35.42	2	W
55	African Spoonbill	*Platalea alba*	Threskiornithidae	7	120	14.58	1.28	W
59	Fulvous Whistling Duck	*Dendrocygna bicolor*	Anatidae	11	1062	22.92	11.29	W

Briton no.	Species common name	Scientific name	Family	Freq[1]	Abund[2]	%Freq[3]	%Abund[4]	Status[5]
60	White-faced Whistling Duck	*Dendrocygna viduata*	Anatidae	8	230	16.67	2.44	W
66	Red-billed Teal	*Anas erythrorhynchos*	Anatidae	1	2	2.08	0.02	W
67	Hottentot Teal	*Anas hottentota*	Anatidae	1	12	2.08	0.13	W
77	African Pygmy Goose	*Nettapus auritus*	Anatidae	3	20	6.25	0.21	W
79	Spur-winged Goose	*Plectropterus gambensis*	Anatidae	1	2	2.08	0.02	W
80	Knob-billed Duck	*Sarkidiornis melanotus*	Anatidae	10	509	20.83	5.41	W
92	Eurasian Marsh Harrier	*Circus aeruginosus*	Accipitridae	8	27	16.67	0.29	Pw
93	[nt]Pallid Harrier	*Circus macrourus*	Accipitridae	5	5	10.42	0.05	P
95	[nt]African Marsh Harrier	*Circus ranivorus*	Accipitridae	7	11	14.58	0.12	W
137	African Fish Eagle	*Haliaeetus vocifer*	Accipitridae	7	11	14.58	0.12	W
194	[nt]Grey-crowned Crane	*Balearica pavonina*	Gruidae	5	24	10.42	0.26	W
199	Common Moorhen	*Galinula chloropus*	Rallidae	14	71	29.17	0.75	W
201	Black Crake	*Limnocorax flavirostra*	Rallidae	26	264	54.17	2.81	W
203	Purple Gallinule	*Porphyrio alleni*	Rallidae	1	3	2.08	0.03	W
225	African Jacana	*Actophilornis africanus*	Jacanidae	22	340	45.83	3.61	W
226	[nt]Lesser Jacana	*Microparra capensis*	Jacanidae	4	17	8.33	0.18	W
231	Little-ringed Plover	*Charadrius dubius*	Charadriidae	2	5	4.17	0.05	PW
233	Ringed Plover	*Charadrius hiaticula*	Charadriidae	1	4	2.08	0.04	PW
245	Long-toed Plover	*Vanellus crassirostris*	Charadriidae	1	2	2.08	0.02	W
249	Spur-winged Plover	*Vanellus sengallus*	Charadriidae	15	84	31.25	0.89	w
252	Common Sandpiper	*Actitis hypoleucos*	Scolopacidae	4	85	8.33	0.9	PW
256	Wood Sandpiper	*Tringa glareola*	Scolopacidae	7	213	14.58	2.26	PW
257	Greenshank	*Tringa nebularia*	Scolopacidae	1	45	2.08	0.48	PW
259	Marsh Sandpiper	*Tringa stagnatilis*	Scolopacidae	2	72	4.17	0.77	PW
262	Common Snipe	*Gallinago gallinago*	Scolopacidae	1	1	2.08	0.01	PW
264	African Snipe	*Gallinago nigripennis*	Scolopacidae	1	85	2.08	0.9	W
270	Curlew Sandpiper	*Calidris ferruginea*	Scolopacidae	1	11	2.08	0.12	PW
272	Little Stint	*Calidris minuta*	Scolopacidae	13	311	27.08	3.3	PW
278	Black-tailed Godwit	*Limosa limosa*	Scolopacidae	2	6	4.17	0.06	PW
282	Black-winged Stilt	*Himantopus himantopus*	Recurvirostridae	9	333	18.75	3.54	pW

Briton no.	Species common name	Scientific name	Family	Freq[1]	Abund[2]	%Freq[3]	%Abund[4]	Status[5]
306	Grey-headed Gull	*Larus cirrocephalus*	Laridae	2	2	4.17	0.02	W
318	White-winged Black Tern	*Chlidonias leucopterus*	Laridae	7	124	14.58	1.32	PW
320	Gull-billed Tern	*Gelochelidon nilotica*	Laridae	3	7	6.25	0.07	PW
464	Giant Kingfisher	*Ceryle maxima*	Alcedinidae	1	2	2.08	0.02	W
465	Pied Kingfisher	*Ceryle rudis*	Alcedinidae	16	140	33.33	1.49	W
466	Malachite Kingfisher	*Alcedo cristata*	Alcedinidae	24	180	50	1.91	W
475	Woodland Kingfisher	*Halcyon senegalensis*	Alcedinidae	22	77	45.83	0.82	An

[1]Number of sites where a species was recorded
[2]Total sums of counts from the 48 wetlands
[3] Percentage of wetlands where the species was observed.
[4]Summed counts from the 48 wetlands divided by the 9,410 bird total
[5]Status of occurrence according to Britton 1980. P – Palearctic migrant, p – Species with at least some palearctic populations, A – Afrotropical migrant, W – Waterbird specialist, w – waterbird non-specialist.
[v]Waterbirds listed as Vulnerable (Bennun and Njoroge, 1996).
[nt]Waterbirds listed as Near-threatened (Bennun and Njoroge, 1996)

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