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Limnological factors that affect waterbird assemblages in semi-arid reservoirs of Tigray National Regional State, northern Ethiopia

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ABSTRACT

Published accounts of the conservation of biodiversity indicate that understanding patterns of species distribution and richness is crucial. However, what drives patterns of species composition in a landscape remains debatable. I examined the relationship between limnological characteristics of reservoirs, morpho-edaphic variables, biological variables, and patterns of bird species richness and distribution. Six limnological, three morpho-edaphic variables, and biological variables were recorded for 35 reservoirs and analyzed by multivariate statistical techniques. To investigate the most important explanatory factors influencing avian species richness and their distribution, redundancy analysis (RDA) was used. A total of 85 bird species from 54 genera, with a mean species richness 14.23 ± 6.72 (mean ± standard deviation) per reservoir, were recorded. The RDA analysis identified two significant RDA axes, and 34.4% of the variation in species richness is explained by environmental variation ($R^2_{adj} = 0.34375$; $P < 0.001$). Bird species richness was positively correlated with the surface area of reservoirs. I showed here that reservoir size and environmental heterogeneity were the important features that affect bird species richness, thus providing an important insight into the ecological relationship between waterbird species richness and the limnological characteristics of reservoirs. The strong positive correlation between species richness and both size and environmental variables underscores the importance of these reservoir features in the management of wildlife conservation. Large, environmentally heterogeneous reservoirs can support more species than small, environmentally homogeneous reservoirs because large, environmentally heterogeneous limnetic ecosystems can provide different resources for nesting, foraging, and roosting habitats for a diversified bird species. The result here also plays a role towards strengthening our knowledge of aquatic bird ecology and the natural history of African-Eurasian Migratory waterbirds.

1. Introduction

Globally, there are approximately 10,928 species of birds distributed in 40 orders, 250 families, and 2322 genera of the class Aves [1]. For many years, ornithologists have examined the geographic distribution, local and regional diversity, and variation of birds [2–4]. Local and regional richness and abundance of bird species are influenced by a variety of variables, such as geographic location, habitat quality, habitat productivity and climatic factors [5–8]. Bird populations around the world are at risk due to human population

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growth, forest destruction, habitat fragmentation, and the loss of suitable habitats [9–13]. How does human-induced ecological and environmental changes affect the abundance and distribution of communities in limnetic ecosystems has long been one of the central themes of ecological studies. For over six decades, a positive relationship between species richness and habitat size (i.e., area) and habitat complexity (i.e., environmental heterogeneity) has been established for terrestrial ecosystems, giving support to the long-established theory of island biogeography [7,14,15]. The concept of island biogeography has also been debated as to whether it could be an option when designing wildlife refuges by wildlife conservation managers, while others still disagree on the use of the model for wildlife conservation. Similarly, studies on aquatic ecosystems have revealed that wetland area, water level, habitat productivity, and heterogeneity are positively related to waterbird species richness and abundance [5,16–19]. It is still unclear, though, which elements are most crucial. In addition, wetland ecosystems are being transformed and decimated by human activities at an increasing rate [20], despite the fact that wetlands are increasingly recognized as critical habitats for birds around the world. Sadly, wetlands are still disappearing as a result of human pressure at the global level, despite the importance of wetland biodiversity [21,22].

In contrast to this global trend of shrinking and losing wetlands, wetlands have been created in Tigray over the past two to three decades as a result of the construction of artificial waterbodies-reservoirs [23]. The construction of such reservoirs has created sizeable wetlands downstream and resulted in favorable microclimate changes in the neighborhood. However, the majority of the research conducted on these limnetic ecosystems involves limnological characteristics [24], phytoplankton community structure [23], fisheries [25], and colonization of these reservoirs by the water flea-Daphnia [26]. There is little information on the avian fauna of these limnetic ecosystems since their construction for irrigation, livestock, and household water consumption purposes. Globally, there are a few studies that compare the diversity and composition of waterbird functional traits between natural, restored, and artificial wetlands [27]. And there are efforts to evaluate the suitability of the use of birds as bioindicators across the globe for different ecological processes and ecosystem health [28,29]. For example, Morelli et al. [30] and Tryjanowski et al. [31] have used Indicator Value (IndVal) analysis to evaluate the suitability of birds as useful indicators of High-Nature-Value farmlands in Italy and Poland, respectively. But to the best of my knowledge, there is no study that has examined the factors that affect bird populations in the limnetic ecosystems of Ethiopia in general and Tigray regional state in particular. Furthermore, it is not known whether modified habitats such as reservoirs and constructed wetlands could act as alternative habitats to attract and sustain bird communities and conserve regional species diversity. A clear understanding of key ecological and limnological factors that affect bird species richness is crucial to the development of limnetic ecosystem management and conservation programs. But much remains to be done in this aspect. This study is focused on bird species richness as an indicator of biodiversity gain triggered by the construction of reservoirs and has the following specific objectives: 1) to assess avian species richness in limnetic ecosystems of different age and size groups; 2) to investigate the effect of limnological and environmental variables on bird species richness and distribution in reservoirs; and 3) to identify the indicator bird species for different age and size groups of the reservoirs in Tigray National Regional State.

2. Materials and methods

2.1. Study area

Tigray National Regional State is located in the northern part of the Federal Democratic Republic of Ethiopia (FDRE, Fig. 1). It is divided into seven administrative zones: the Western Zone, the Northwestern Zone (NW), the Central Zone, the Eastern Zone, the

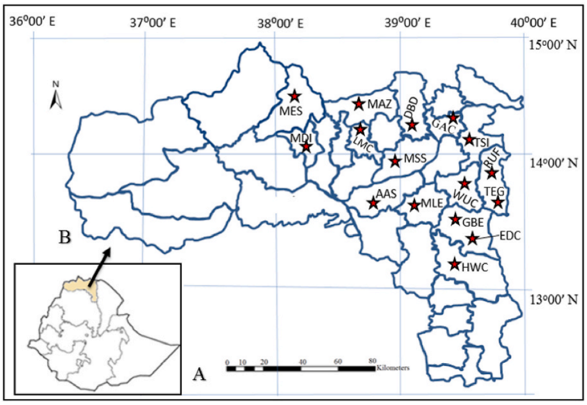

Fig. 1. Map of Ethiopia with Tigray National Regional State highlighted in grey (A) and districts of Tigray National Regional State, with the location of the reservoirs sampled from each district indicated in a star (B). MES = Meskebet; MDI = Mai-Dimu; MAZ = Mihtsab Azmati; Laelay Maichew Cluster (LMC): Mai Nigus (MNG) and Mai Seye (MSY); MSS = Mai Sessela; DBD = Dibdibo; AAS = Adi Asma'e; Ganta-afeshum Cluster (GAC): Bokoro (BOK), Dibla (DIB) and Enda Gabriel (EGA); TSI = Tsinkanet; RUF = Ruba Feleg; TEG = Teg'hane; Wukro cluster (WUC): Laelay Wukro (LWK) and Korir (KOR); MLE = Mai Leba; GBE = Gereb Beati; HWC = Hintalo Wajerat Cluster (HWC): AGE = Adi Gela; AKE = Adi Kenafiz; BET = Betequa; DAM = Dur Anbasa; GMI = Gereb Mihiz; GSE = Gum Selassa; HAI = Haiba; MDE = Mai Delle; MGI = Mai Gassa I; MGII = Mai Gassa II; MEA = Meala; SHI = Shilanat IV and Enderta Cluster (EDC): HAS = Hashenge; ADA = Adi Amharay; HWD = Hizaeti Wedi Cheber; EQU = Era Quihila; GAW = Gereb Awso.

Southeastern Zone (SE), the Southern Zone, and Mekelle Special Zone, which are further divided into more than 47 administrative districts (Fig. 1). The region has four traditional agro-ecological classifications: "Qhola" (below 1500 m a.s.l.), "Weyna Degu'a" (1500–2300 m a.s.l.), "Degu'a" (2300–3200 m a.s.l.), and "Wurch/Alelama" (above 3200 m a.s.l.). The "Tsibet Sky Island", in the Southern Zone of Tigray National Regional State, is the highest mountain range in the region, with its peak reaching 3960 m a.s.l., while the lowest point in the region is around 500 m a.s.l., located in the Tekeze valley, in the Western Zone of Tigray.

The rainfall in Tigray is erratic and highly seasonal, resulting in moisture stress that hampers rain-fed agriculture. Over the past four decades, the regional government of Tigray's top priority has been the construction of reservoirs to support rain-fed agriculture through irrigation. With the main aim of bringing food self-sufficiency to the area through irrigation, more than 60 reservoirs have been constructed over the past four decades [23,24]. Here, 35 reservoirs were included in a study of the avifauna of the limnetic aquatic ecosystem of the region (see Table S1 in supporting information). These reservoirs were specifically chosen according to prior knowledge of each site [25,26,32]. The age of the reservoirs ranges from the newest, Mihtsab Azmati reservoir (MAZ, 5 years), to the oldest, Bokoro reservoir (BOK, 44 years). Additionally, they differ in terms of elevation (1512–2747), water surface (1.78–45.41 ha), and water depth (1–13.7 m).

For each reservoir, I have recorded three physical habitat variables: reservoir area, water depth, elevation, and six water quality parameters: pH, nutrient concentration (total nitrogen and total phosphate), water turbidity, water temperature, and electrical conductivity that are known to influence ecological processes and species abundance in freshwater wetlands and lakes [18,33–35]. Biological variables such as the presence and absence of fish, macrophytes, and the presence or absence of forest edges were recorded and coded into an appropriate format for analysis. Limnological characteristics of each reservoir: the reservoir's morphometry (altitude, area and maximum depth) were obtained from Asmelash et al. [23] and Haileselasie et al. [26], and water chemistry variables: water temperature (°C), pH, and electrical conductivity (EC, μS/cm) were measured in the field using portable pH/EC multi-meters. Whereas integrated water samples were collected and brought to the Aquatic Ecology Laboratory (Mekelle University, Tigray) for determination of total phosphorus (TP, μg/l) and total nitrogen (TN, μg/l) in the laboratory using standard methods stated in Nelson and Sommers [36].

2.2. Bird surveys

Birds sighted utilizing limnetic ecosystems during the survey of 35 reservoirs were counted to provide data for this study. Depending on the size of the water body, observers either walked along the reservoir's perimeter or motored around each reservoir to record the birds they saw using limnetic ecosystems. Then birds were identified to a species level based on the bird's field guide for East Africa, birds of sub-Saharan Africa, and a country-specific checklist [37–40]. Then, based on the collected data, gamma diversity, i.e., the total number of bird species observed throughout the entire sampling period in the region, and alpha diversity, i.e., the number of bird species recorded in each reservoir, were calculated. The frequency of occupancy, or how many reservoirs a specific bird taxon (family or species) is detected in, was also calculated from the presence and absence data collected during the sampling campaigns. The English names and taxonomy of birds reported here follow the International Ornithological Congress (IOC) standard format [1].

2.3. Data analysis

Differences in limnological variables between reservoirs are visualized by principal component analyses on the residuals of the full limnological data set. Principal components were extracted from covariance matrices using the function rda in the vegan package of the R software [41]. The eigenvalues and percentage of variance for each axis were used to retain the number of significant PC axes for further analysis. And the Euclidean distance after standardizing the variables, followed by Ward clustering, is used to display a plot of the first two PC axes of limnological components.

To determine the most significant explanatory factors affecting the richness and distribution of bird species, species richness data was subjected to a multiple regression analysis at limnological variables, habitat physical variables, biological variables, and the age of the reservoirs. And then the statistical significance of the impact of each variable is examined using the Monte Carlo permutation test using 999 permutations. Besides, the scores of species (alpha diversity) and environmental variables resulting from the ordination are used to build a bi-plot that illustrates the relationships between environment and bird species richness. To describe the environmental preferences of particular species, redundancy analysis (RDA) in R software [41] was applied. The function that partitions the variation-varpart in the vegan R package [42] using adjusted R-squared (R^2_{adj}) in redundancy analysis ordination (RDA) is used to disentangle the effect of these variables in species – limnological variables– habitat physical variables-biological variables-geographic distance - age variation partitioning by partial regression.

I examined three habitat variables: wetland area, water depth, and age of the reservoirs as predicators of waterbird distribution, and presence of species in (species richness) reservoirs as response variables. In order to study the indicator species of typical of reservoir categories (i.e., reservoirs grouped by age, surface area, and depth), I applied an indicator species analysis (IndVal analysis) using the 'indicspecies' module in R [43] to measure the association. For the indicator species analysis, I used species occurrence from 35 reservoirs (a presence and absence data set as a community matrix) and the classification of the reservoirs into groups, which represent age group (young vs. old), surface area (small vs. large), and depth (deep vs. shallow) categories. The statistical significance of this relationship between species and group category was tested using a permutation test.

3. Results

3.1. Limnological characteristics and taxonomic richness

Principal component analysis (PCA) identified three major axes of environmental variation (axes that explain more than 10% of the variation). PCA reduced the data set to three components that explained 64.27% of the variance in the original variables. The first and second axes of the PCA explained 51.07% of the total variation observed. PC1 explained 28.69% of the variation and can be interpreted as a measure of altitude, surface area, total nitrogen (TN) and total phosphorus (TP) (Fig. 2 and Table S2 in the supplementary information). PC2 explained 22.38% of the limnological variation and was loaded heavily by electrical conductivity, pH, and reservoir depth. PC3, which explained 13.2% of the variation, was loaded mostly by water temperature and transparency (see Table S2 in the supplementary information). As can be seen in Fig. 2, three major clusters of reservoirs are created based on the PCA components. Cluster 1 is composed of six lowland reservoirs (i.e., in the Weyna Degu'a agroclimate, 1500–2300 m.a.s.l.) and deep reservoirs. Cluster 2 is composed of 12 highland reservoirs, mostly with high nutrient concentrations. With the exception of Dibdibo (DBD) reservoir, all reservoirs in this cluster are highland reservoirs (i.e., fall within the Degu'a agroclimate), while Cluster 3 is composed of 17 reservoirs of mixed elevation but mostly with high water transparency and a low value for total nitrogen (TN) (Fig. 2).

Avian fauna associated with limnetic aquatic ecosystems from 35 reservoirs is presented in Table 1. A total (γ-diversity) of 85 bird species from 54 genera, 25 families, and 15 bird orders were recorded during the study period (Table 1 and Table S3 in the supplementary information). Most of the waterbirds (60%) recorded are all-year residents, and 4.71% (n = 4 bird species) are intra-African migrants and visitors. Thirty of the waterbirds (35.29%) recorded are Palaearctic migrants/winter visitors (see Table S3 in the supplementary information). Out of the total bird species recorded, five species: Black-Tailed Godwit (*Limosa limosa),* Ferruginous Duck (*Aythya nyroca*), Lesser Flamingo (*Phoeniconaias minor*), Maccoa Duck (*Oxyura maccoa*), and Pallid Harrier (*Circus macrourus*), fall under the near threatened (NT) IUCN conservation status designations. Two species, the Hooded Vulture (*Necrosyrtes monachus*) and Common Pochard (*Aythya ferina*) fall under critically endangered (CR) and vulnerable (VU) conservation status designations, respectively. While the rest (91.8%) of the birds recorded are of least concern (LC) under the IUCN conservation status designations

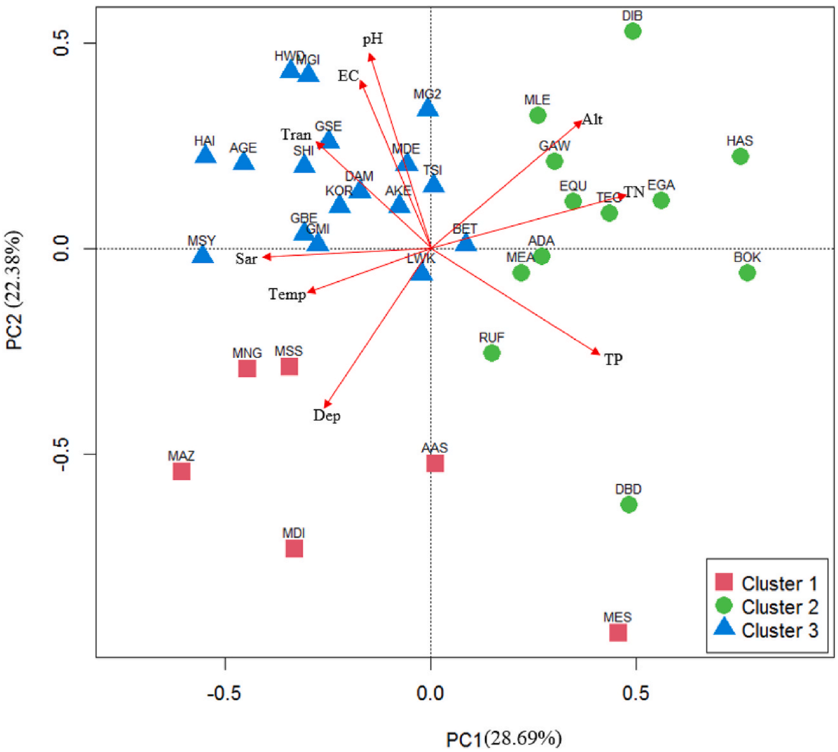

Fig. 2. Principal components analysis biplot of the reservoir's characteristics with overlaid clustering results. Reservoir's three-letter code: MES = Meskebet; MDI = Mai-Dimu; MAZ = Mihtsab Azmati; MNG = Mai Nigus; MSY = Mai Seye; MSS = Mai Sessela; DBD = Dibdibo; AAS = Adi Asma'e; BOK = Bokoro; DIB = Dibla; EGA = Enda Gabriel; TSI = Tsinkanet; RUF = Ruba Feleg; TEG = Teg'hane; LWK = Laelay Wukro; KOR = Korir; MLE = Mai Leba; GBE = Gereb Beati; AGE = Adi Gela; AKE = Adi Kenafiz; BET = Betequa; DAM = Dur Anbasa; GMI = Gereb Mihiz; GSE = Gum Selassa; HAI = Haiba; MDE = Mai Delle; MGI = Mai Gassa I; MGII = Mai Gassa II; MEA = Meala; SHI = Shilanat IV; HAS = Hashenge; ADA = Adi Amharay; HWD = Hizaeti Wedi Cheber; EQU = Era Quihila and GAW = Gereb Awso And codes for environmental variables: Dep = reservoir's depth, Temp = water temperature, sar = surface area, Tran = transparency, EC = electrical conductivity, alt = altitude, TN = total nitrogen, and TP = total phosphorus.

Table 1
Taxonomic richness and details of waterbird species recorded across 35 reservoirs during the study period in Tigray National Regional State. †row number for each bird order adapted from the International Ornithological Congress (IOC) World Bird List (10.1) [1]††Common names follow that of IOC format; *species recorded in/at the perimeter of the reservoirs thus are not water specialist birds; §number of reservoirs the species was recorded from;†††conservation status designation by the International Union for Conservation of Nature (IUCN): Near Threatened (NT), Vulnerable (VU), Critically Endangered (CR), and Least Concern (LC) (IUCN, 2019) and§ the number of reservoirs in which the bird order and species were recorded.

IOC-row†	Bird order **English name††**	**Zoological name**	**Family**	**§Occupancy**	**††† IUCN status**
231	**Galliformes**			1	
	Helmeted Guineafowl*	*Numida meleagris*	Numididae	1	LC
1261	**Anseriformes**			35	
	Common Pochard	*Aythya ferina*	Anatidae	11	VU
	Egyptian Goose	*Alopochen aegyptiaca*	Anatidae	35	LC
	Eurasian Teal	*Anas crecca*	Anatidae	2	LC
	Eurasian Wigeon	*Mareca penelope*	Anatidae	1	LC
	Ferruginous Duck	*Aythya nyroca*	Anatidae	2	NT
	Fulvous Whistling Duck	*Dendrocygna bicolor*	Anatidae	1	LC
	Gadwall	*Mareca strepera*	Anatidae	1	LC
	Garganey	*Anas querquedula*	Anatidae	1	LC
	Maccoa Duck	*Oxyura maccoa*	Anatidae	5	NT
	Northern Pintail	*Anas acuta*	Anatidae	5	LC
	Northern Shoveler	*Anas clypeata*	Anatidae	19	LC
	Red-billed Teal	*Anas erythrorhyncha*	Anatidae	2	LC
	Southern Pochard	*Netta erythrophthalma*	Anatidae	1	LC
	Tufted Duck	*Aythya fuligula*	Anatidae	2	LC
	Yellow Billed Duck	*Anas undulata*	Anatidae	10	LC
3451	**Cuculiformes**			1	
	Eastern Grey Plantain-eater*	*Crinifer zonurus*	Musophagidae	1	LC
4852	**Gruiformes**			15	
	Eurasian Coot	*Fulica atra*	Rallidae	9	LC
	Red-knobbed Coot	*Fulica cristata*	Rallidae	14	LC
5340	**Podicipediformes**			25	
	Great Crested Grebe	*Podiceps cristatus*	Podicipedidae	14	LC
	Little Grebe	*Tachybaptus ruficollis*	Podicipedidae	23	LC
5416	**Phoenicopteriformes**			1	
	Lesser Flamingo	*Phoeniconaias minor*	Phoenicopteridae	1	NT
5427	**Charadriiformes**			35	
	African Snipe	*Gallinago nigripennis*	Scolopacidae	1	LC
	African Wattled Lapwing	*Vanellus senegallus*	Charadriidae	6	LC
	Black-tailed Godwit	*Limosa limosa*	Scolopacidae	1	LC
	Black-winged Lapwing	*Vanellus melanopterus*	Charadriidae	1	LC
	Black-winged Stilt	*Himantopus himantopus*	Recurvirostridae	18	LC
	Collared Pratincole	*Glareola pratincola*	Glareolidae	1	LC
	Common Greenshank	*Tringa nebularia*	Scolopacidae	20	LC
	Common Sandpiper	*Actitis hypoleucos*	Scolopacidae	28	LC
	Common Snipe	*Gallinago gallinago*	Scolopacidae	3	LC
	Curlew Sandpiper	*Calidris ferruginea*	Scolopacidae	1	LC
	Egyptian Plover	Pluvianus aegyptius	Pluvianidae	1	LC
	Green Sandpiper	*Tringa ochropus*	Scolopacidae	3	LC
	Gull-billed Tern	*Sterna nilotica*	Sternidae	7	LC
	Little Tern	*Sterna albifrons*	Sternidae	1	LC
	Marsh Sandpiper	*Tringa stagnatilis*	Scolopacidae	3	LC
	Pied Avocet	*Recurvirostra avosetta*	Recurvirostridae	3	LC
	Ruff	*Calidris pugnax*	Scolopacidae	2	LC
	Senegal Thick-knee	*Burhinus senegalensis*	Burhinidae	6	LC
	Spot-Breasted Lapwing	*Vanellus melanocephalus*	Charadriidae	1	Endemic
	Spotted Thick-knee	*Burhinus capensis*	Burhinidae	1	LC
	Spur-winged Lapwing	*Vanellus spinosus*	Charadriidae	20	LC
	Terek Sandpiper	*Xenus cinereus*	Scolopacidae	1	LC
	Three-banded Plover	*Charadrius tricollaris*	Charadriidae	21	LC
	Water Thick-knee	*Burhinus vermiculatus*	Burhinidae	1	LC
	White-winged Tern	*Chlidonias leucopterus*	Sternidae	4	LC
	Wood Sandpiper	*Tringa glareola*	Scolopacidae	10	LC
	Common Redshank	*Tringa totanus*	Scolopacidae	1	LC
6663	**Ciconiiformes**			16	
	Abdim's Stork	*Ciconia abdimii*	Ciconiidae	7	LC
	African Open-billed Stork	*Anastomus lamelligerus*	Ciconiidae	1	LC
	Black Stork	*Ciconia nigra*	Ciconiidae	3	LC
	Marabou Stork	*Leptoptilos crumenifer*	Ciconiidae	1	LC
	White Stork	*Ciconia ciconia*	Ciconiidae	10	LC
	Woolly-necked Stork	*Ciconia episcopus*	Ciconiidae	1	LC

(*continued on next page*)

Table 1 (*continued*)

IOC-row[†]	Bird order **English name**[††]	**Zoological name**	**Family**	[§]**Occupancy**	[†††] **IUCN status**
	Yellow-billed Stork	*Mycteria ibis*	Ciconiidae	6	LC
6696	**Suliformes**			4	
	White-breasted Cormorant	*Phalacrocorax lucidus*	Phalacrocoracidae	4	LC
6829	**Pelecaniformes**			32	
	African Sacred Ibis	*Threskiornis aethiopicus*	Threskiornithidae	12	LC
	African Spoonbill	*Platalea alba*	Threskiornithidae	2	LC
	Black-headed Heron	*Ardea melanocephala*	Ardeidae	1	NT
	Cattle Egret	*Bubulcus ibis*	Ardeidae	11	LC
	Glossy Ibis	*Plegadis falcinellus*	Threskiornithidae	2	LC
	Goliath Heron	*Ardea goliath*	Ardeidae	2	LC
	Great Egret	*Egretta alba*	Ardeidae	4	LC
	Great White Pelican	*Pelecanus onocrotalus*	Pelecanidae	4	LC
	Grey Heron	*Ardea cinerea*	Ardeidae	28	LC
	Hamerkop	*Scopus umbretta*	Scopidae	8	LC
	Little Egret	*Egretta garzetta*	Ardeidae	15	LC
	Pink-backed Pelican	*Pelecanus rufescens*	Pelecanidae	14	LC
	Purple Heron	*Ardea purpurea*	Ardeidae	5	LC
	Wattled Ibis	*Bostrychia carunculata*	Threskiornithidae	9	Endemic
	Intermediate Egret	*Egretta intermedia*	Ardeidae	3	LC
7123	**Accipitriformes**			6	
	African Fish Eagle	*Haliaeetus vocifer*	Accipitridae	1	LC
	Hooded Vulture*	*Necrosyrtes monachus*	Accipitridae	2	CR
	Long-crested Eagle*	*Lophaetus occipitalis*	Accipitridae	1	LC
	Osprey	*Pandion haliaetus*	Pandionidae	1	LC
	Pallid Harrier	*Circus macrourus*	Accipitridae	1	NT
	Yellow-billed Kite*	*Milvus aegyptius*	Accipitridae	3	LC
8972	**Coraciiformes**			4	
	Giant Kingfisher	*Megaceryle maxima*	Alcedinidae	1	LC
	Malachite Kingfisher	*Alcedo cristata*	Alcedinidae	1	LC
	Pied Kingfisher	*Ceryle rudis*	Alcedinidae	2	LC
9558	**Piciformes**			1	
	African Grey Woodpecker*	*Dendropicos goertae*	Picidae	1	LC
11,220	**Psittaciformes**			1	
	Rose-ringed Parakeet*	*Psittacula krameri*	Psittacidae	1	LC
12,253	**Passeriformes**			3	
	African Pied Wagtail	*Motacilla aguimp*	Motacillidae	1	LC
	White Wagtail	*Motacilla alba*	Motacillidae	2	LC

(Table 1).

Charadriiformes had the highest number of recorded taxa (7 families, 15 genera, 27 species) followed by Pelecaniformes (4 families, 9 genera, 15 species) (Table 1). Within the recorded Charadriiformes, the Scolopacidae (Sandpipers and allies) was the most widespread family of that order (12 species). Of all the families recorded, Anatidae (order: Anseriformes) was the family with the most recorded genera (7 genera; 15 species; including geese, ducks, teals), followed by the Scolopacidae (order: Charadriiformes) (6 genera; 12 species; including sandpipers and snipes). The Ardeidae (herons and egrets), Ciconiidae (storks) and Accipitridae (raptors) were the next in number of families recoded with 8, 7 and 5 species per family, in that respective order (Table 1).

Individual bird species occurred at 1 (2.86%) to 35 (100%) of the reservoirs (Table 1). From the 35 reservoirs sampled, the highest frequency of occupancy have been recorded for Egyptian Goose (*Alopochen aegyptiaca*) followed by: Common Sandpiper (*Actitis hypoleucos*) and Grey Heron (*Ardea cinerea*) recorded from 28 to 26 reservoirs, respectively (Table 1 and see Table S3 in supporting information). Three of the Near-threatened birds recorded in this study were from a single reservoir while the two other birds in this category status: Ferruginous Duck (*Aythya nyroca*) and Maccoa Duck (*Oxyura maccoa*) are recorded from two and five reservoirs, respectively (Table 1). The spatial distribution of the two endemic species recorded was also different. The Wattled Ibis (*Bostrychia carunculata)* is recorded from nine reservoirs whereas Spot-breasted Lapwing (*Vanellus melanocephalus*) is recorded from Mai Nigus reservoir only (Table 1 and see Table S3 in supporting information). The spatial distribution of the four intra-African migrants recorded: African Openbill (*Anastomus lamelligerus*), Southern Pochard (*Netta erythrophthalma*), Abdim's Stork (*Ciconia abdimii*) and Pied Avocet (*Recurvirostra avosetta*) did not show a uniform pattern. The first two species were recorded from a single reservoir each while Abdim's Stork and Pied Avocet were recorded from seven and three reservoirs, respectively (Table 1 and see Table S3 in supporting information).

The alpha (α) diversity of reservoirs varies from 3 to 32 with 14.23 ± 6.72 (mean ± standard deviation) birds per reservoir. Mai Nigus (n = 32 species) and Tsinkanet (n = 26 species) had the highest bird species recorded, followed by Mai Gassa I reservoir (n = 23 species) and Haiba reservoir (22 species) (Fig. 3A). Two spatial distribution pattern of species richness (α-diversity) of waterbird population are clearly detected. The first pattern is within Northern cluster where the central reservoirs have a higher alpha diversity while northern reservoirs have relatively lower alpha diversity when plotted along the geographic location of reservoirs (Fig. 3B). The second pattern is within the southern Tigray where higher alpha diversity is observed in the center while reservoirs in the peripheries have lower alpha diversity (Fig. 3B). The second pattern becomes clearly visible after removing Haiba reservoir from the data set which is connected to Meala reservoir.

The results of the association between species patterns and combinations of groups of reservoirs are presented in Table 2. In a singleton indicator species analysis, only the Wood Sandpiper (*Tringa glareola*) was found to be strongly and significantly associated with the old reservoir age group (stat = 0.669, $P < 0.05$) and small reservoir (stat = 0.647, $P < 0.05$, Table 2). The simultaneous occurrence of sets of species (i.e., species combinations) revealed that a combination of two avian species is a good indicator of the first age group (i.e., young reservoirs) as it occurs in sites belonging to this group only (i.e., A = 1.0000, Table 2). While another two combinations of species, *Charadrius tricollaris* + *Tringa glareola and Tringa glareola* + *Anas undulata*, revealed themselves to be good indicators of the second age group (i.e., old reservoirs; A = 1.0000, Table 2). The multilevel pattern analysis indicated that two species are significantly associated with young reservoirs, while eight avian species have been associated with older reservoirs (Table 2). In a single species analysis, only four bird species were found as indicators of large-sized reservoirs (Table 2), and a single bird species was significantly diagnostic of small-sized reservoirs in Tigray. Small-sized reservoirs are represented by only one indicator species (*Tringa glareola,* Table 2), while large-sized reservoirs are represented by four indicator species. However, the number of species associated with the reservoir size group gave rise to 44 bird species in the multilevel species combination pattern analysis. Five species were

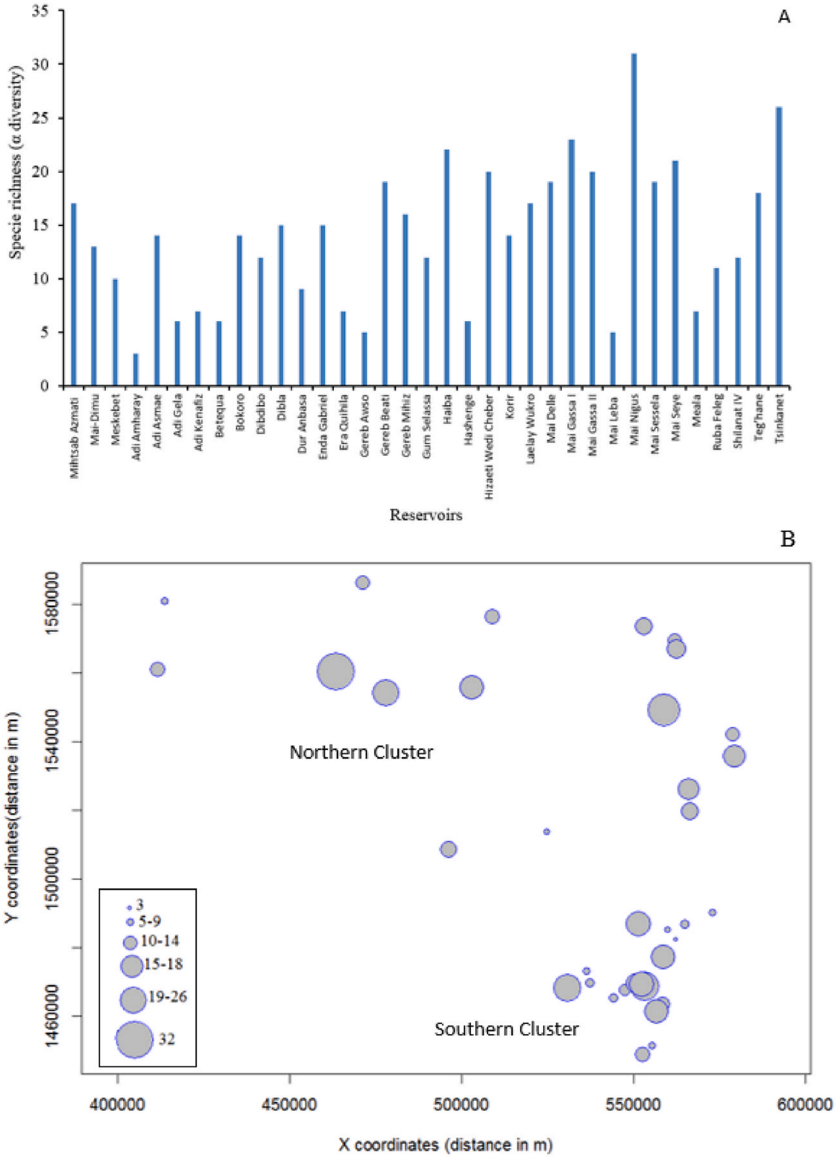

Fig. 3. Specie richness (α diversity) of the respective reservoir investigated during the study period (A) and the pattern of species richness of waterbird populations inhabiting reservoirs sampled in Tigray (B). The species richness with respect to geographic location of the reservoirs is plotted along X–Y coordinates; the size of the circle is proportional to species richness of each reservoir.

Table 2
Results of multilevel pattern analysis of association between species patterns and combinations of groups of reservoirs using the Association function, IndVal.g [44,45]. †Indicator value components: "A" is the positive predictive value of the species as an indicator of the site group (i.e., the specificity); 'B′ is the fidelity or sensitivity of the species as an indicator of the target site group. Only species with a significant P value are shown.

Reservoir's			Indicator value index†			
Group	Category	Species/Species combination	A	B	stat	*P*-value
Age	Young reservoirs, number of species = 2					
		Ciconia abdimii + *Threskiornis aethiopicus*	1.00	0.2353	0.485	0.036*
		Ciconia ciconia + *Mycteria ibis*	1.00	0.2353	0.485	0.046*
	Old reservoirs, number of species = 8					
		Tringa glareola	0.8947	0.5	0.669	0.007**
		Alopochen aegyptiaca + *Tringa glareola*	0.8947	0.5	0.669	0.007**
		Tringa nebularia + *Tringa glareola*	0.8686	0.3889	0.581	0.049*
		Actitis hypoleucos + *Tringa glareola*	0.8686	0.3889	0.581	0.044*
		Ardea cinerea + *Tringa glareola*	0.8686	0.3889	0.581	0.044*
		Fulica cristata + *Tringa glareola*	0.8686	0.3889	0.581	0.044*
		Charadrius tricollaris + *Tringa glareola*	1.000	0.3333	0.577	0.025*
		Tringa glareola + *Anas undulata*	1.000	0.2778	0.527	0.037*
Size	Small reservoir, number of species = 1					
		Tringa glareola	0.8834	0.4737	0.647	0.006**
	Large reservoir, number of species = 4					
		Podiceps cristatus	0.748	0.625	0.684	0.023**
		Bubulcus ibis	0.7037	0.625	0.663	0.046*
		Egretta garzetta	0.7037	0.6250	0.663	0.039*
		Phalacrocorax lucidus	1.00	0.25	0.5	0.033*
Depth	Deep reservoirs, number of species = 3					
		Mycteria ibis	1.0000	0.3333	0.577	0.025*
		Alopochen aegyptiaca + *Mycteria ibis*			0.577	0.023 *
		Vanellus spinosus + *Mycteria ibis*			0.527	0.049 *
	Shallow reservoirs, number of species = 0					

associated with shallow reservoirs, while 39 species combinations were associated with deep reservoirs. The complete output, with the results of the IndVal analysis, is provided in Table S4 in the supplementary materials. Similarly, a single species analysis gave no indicator species for the depth category of reservoirs, but a multi-species IndVal analysis gave four species as indicators of deep reservoirs in Tigray (Table 2).

3.2. Relationship between bird species richness and limnological variables

Redundancy analysis (RDA) revealed two significant RDA axes, and environmental variation accounts for 34.4% of the variation in

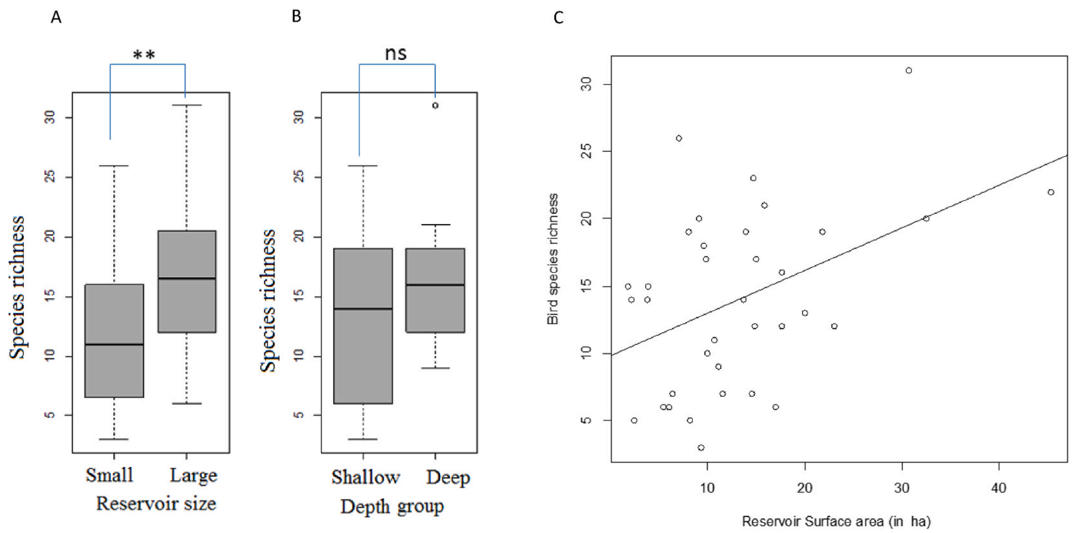

Fig. 4. Relationship between bird species richness (α diversity) and reservoir's morphometry variables: surface area (in hectares) and depth group (in meters). Panels A and B indicate a relationship between species richness and reservoir size and depth. Boxes represent the inter-quartile range, whiskers represent the minimum and maximum observations (A and B). Panel C indicates the relationship between bird species richness and the surface area (in hectares) of reservoirs. The significance level: ** significantly different at $p < 0.01$ and ns = non-significant $p = 0.45$.

species richness of the reservoirs ($R^2_{adj} = 0.34375$; $P < 0.001$). Among the limnological variables elevation, water depth, pH, and nutrients were the four variables that best explained the variance in bird species richness observed. Several of the studied environmental variables showed a clear correlation with the presence of particular bird species (Fig. S1 in supplementary information). A strong positive relationship between species richness and the size of the reservoir is detected, but not the depth (Fig. 4A–C). That is, bigger reservoirs did support a higher number of bird species (Fig. 4B). However, no significant relationship between depth of reservoirs and species richness was detected (Fig. 4B).

The RDA indicates that a significant portion of the variation in species composition is explained by both biological variables (BV) and environmental variables (ENV) ($R^2_{adj} = 0.18$, $p < 0.001$). If only environmental and biological variables are used in the RDA, environmental variation explained 9.5% of the variation in species composition ($R^2_{adj} = 0.0953$, $p < 0.001$), whereas biological variables (BV) explained about 8.9% of the variation in species composition ($R^2_{adj} = 0.089$, $p < 0.001$; Fig. 5A). Among the environmental variables, elevation, depth, pH, transparency, and TP contributed significantly to explaining the variation in species composition in the studied reservoirs. In a partial RDA analysis, the complete model (ENV ∪ BV) accounted for about 18% of the variation in species composition ($R^2_{adj} = 0.1799$, $p < 0.001$; Fig. 5A), with environmental variables ($R^2_{adj} = 0.091$, $p < 0.001$) being most important. But a significant portion of the variation in species composition was also explained by pure biological variables ($R^2_{adj} = 0.085$, $p < 0.01$), while shared environmental and biological variables contributed less than 1% (Fig. 5A and see Table S5 and Fig. S2 in supporting information). A large part of the variation in species composition, however, remained unexplained ($R^2_{adj} = 0.82$; Fig. 5A).

Including age of reservoirs (AGE) as an independent variable in the partial RDA did change the percentage of variation explained by environmental variables ($R^2_{adj} = 0.107$, $p < 0.001$; Fig. 5B) and biological variables ($R^2_{adj} = 0.074$, $p < 0.001$) differently. It did, reduce

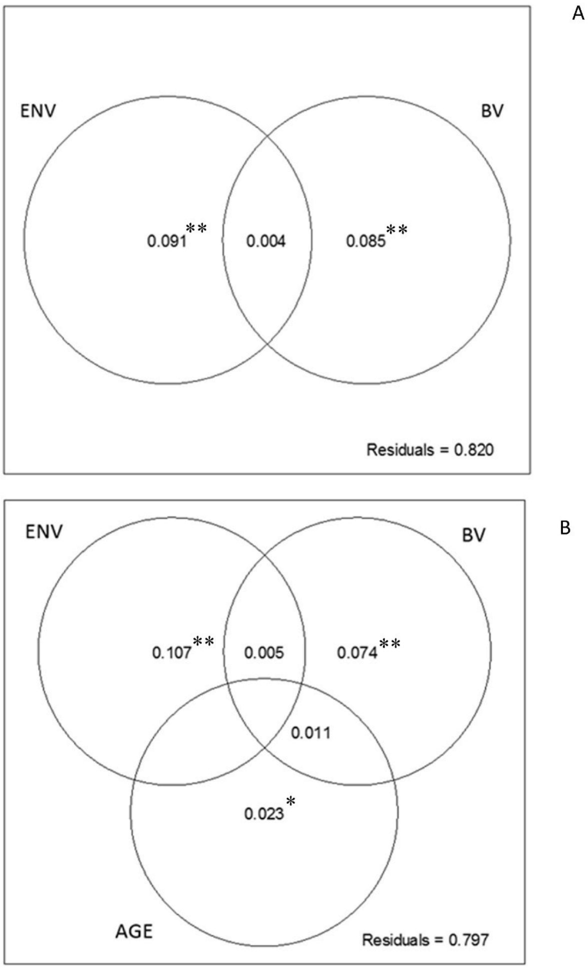

Fig. 5. Venn diagram illustrating the results of variation partitioning from the partial redundancy analysis (pRDA) of the bird species composition along an age gradient of reservoirs in Tigray National Regions State, Northern Ethiopia. The pRDA shows the unique and shared contribution of biological descriptors (BV), environmental heterogeneity (ENV), and approximate age (AGE) of reservoirs (AGE) to the variation in bird species composition observed in the reservoirs. A) Results of the pRDA based on two variables; B) pRDA with three variables: ENV, BV, and AGE as independent variables. The numbers in the Venn diagram represent the fraction of variation in species composition that is explained by each independent variable. Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05.

the variation explained by biological descriptors (BV), and the pure effect of BV is down to 7.4% ($R^2_{adj} = 0.074$, $p < 0.001$; Fig. 5B). The combined effect of ENV, AGE and BV ($R^2_{adj} = 0.203$) was higher than that of the effect without age. The pure effect of AGE was small but statistically significant ($R^2_{adj} = 0.023$, $p < 0.05$; Fig. 5B) and its effect was also confounded with BV effects (Fig. 5B; see also Table S5 and Fig. S2 in supporting information). Only a small fraction of the variation was shared among BV descriptors and environmental heterogeneity ($R^2_{adj} = 0.005$, $p < 0.001$; Fig. 5B).

The global model, using ENV, BV, AGE and geographic location of each reservoir (SPACE) as an independent variables in the partial RDA did not change the percentage of variation explained by environmental variables ($R^2_{adj} = 0.107$, $p < 0.001$; Fig. 5B) and biological variables ($R^2_{adj} = 0.074$, $p < 0.001$). However, the model indicated the marginal effect of SPACE on the bird species richness to be 5.6%. Out of these, 4% is pure effect of SPACE and 1.6% is confounded with effect of AGE and BV variables (see Appendix S5 in supporting information).

4. Discussion

The 35 reservoirs surveyed showed age gradients and structural habitat heterogeneity, including variations in size, elevation, and limnological traits, among others. Here, I demonstrate the significance of these reservoirs as important repositories for bird species, including species designated as Near Threatened (NT), Vulnerable (VU), Critically Endangered (CR) under the International Union for Conservation of Nature (IUCN) conservation status [46], and endemic birds. In the face of unprecedented habitat loss and degradation of natural wetlands, it can be contended that such artificial waterbodies can play an important role in waterbird conservation. Ma et al. [47] argued the need for maintaining natural wetlands as a priority for waterbird conservation. However, they also showed that when natural wetlands are not available and/or of poor quality, birds are able to use the artificial wetlands in Chongming Island, China. The finding of Ma et al. [47] is indeed in line with the results of this study, where artificial waterbodies (i.e., reservoirs) harbored 85 species of birds, indicating that these reservoirs and their associated wetlands have the capacity to maintain high avian diversity. In line with the results presented here, other studies have likewise indicated that urban reservoirs and artificial ponds harbor waterbird communities and act as refugia for waterbirds [27,47–49]. A comparative study of artificial and created/restored wetlands in Spain has also confirmed that restored and artificial wetlands do have a similar conservation value and can assure the maintenance of key ecological processes [50]. Recently, studies have indicated that ponds (aquatic ecosystems of size ranging from 1 m^2 up to 2 ha and less than 8 m depth) have great potential to support a high richness of aquatic species [51].

This study found a positive correlation between bird species richness and reservoir area, which is consistent with earlier research that found wetland area and habitat heterogeneity to be the most significant factors influencing aquatic bird species richness and abundance [4,18,52,53]. The significant difference in species richness between large and small reservoirs observed in this study is also in line with the long-established theory of island biogeography [54] which argues that large areas (large-sized reservoirs, in our case) are expected to contain more species (i.e., higher taxonomic richness). The rationale behind this area-richness relationship is that larger area is likely to have more habitats, hence niches, to support a greater variety of species [54,55].

Community ecology and population genetic research have shown that spatial variation in species composition is the result of environmental sorting, dispersal limitation, and historical factors at different temporal scales [56–58]. Here, I have established that environmental variables are responsible for the highly significant variation in bird species richness among reservoirs, and that the age of the reservoir also has small but significant effect. This result is in agreement with previous research that showed that patterns of beta diversity are sensitive to environmental and historical factors [56]. The small but significant effect of reservoir age on bird species richness is also in line with the long-established meta-population theory [59], which contends that as a habitat ages, it becomes more heterogeneous and offers a variety of resources for nesting, foraging, and other activities for different bird species [7,9,17,27].

Despite the fact that positive correlations between habitat area and species richness have long been established [60], what drives patterns of species composition in a landscape, however, remains debatable. The concept of island biogeography has also been proposed as an option when designing wildlife refuges by wildlife conservation managers, while others still disagree on the use of the model for wildlife conservation. For example, Merckx et al. [61] argued that habitat amount, not patch size, drives species richness against the long-established island biogeography [54]. Contrary to the theory of island biogeography, Scheffer et al. [53] have suggested that small habitat size and isolation promote species richness in shallow lakes and ponds. While others have argued that larger habitats (or islands) accumulate a higher number of species [54]. In favor of this argument, studies have indicated that wetland area, vegetation cover, and structural heterogeneity of habitat are the most important features that affect wetland bird richness and abundance [3,5,6,60]. The result of this study provides additional evidence in favor of the later argument. However, mere size is not significant, but the possible presentation of large habitats accompanied by an increase in habitat heterogeneity does support greater species richness.

A previous study in Merced County, California [62] showed that water depth predicts the presence of species in wetlands. This investigation did not support the positive link between reservoirs' depth and bird species richness, in contrast to a prior study that found a favorable relationship between bird richness and lake depth [63,64]. This might be a result of the species-specific influence of reservoir depth [6,62].

With regard to the distribution of the waterbirds, two patterns are apparent in this study. Some species are widely distributed water specialists, while others are restricted in their distribution but also non-specialists or opportunists. Such a pattern of distribution has been reported previously elsewhere [18]. Some of the bird species recorded in this study occurred in almost all the reservoirs, thus being generalists. While others are reported from a single reservoir with specific habitat features such as the presence of settlements or large wetland forests downstream or in close proximity to the reservoir. Some reservoirs are very close to residential areas (example: Bokoro and Mai Sessela) or have very large wetlands downstream (example: Meskebet reservoir). This might be responsible for the presence of the Eastern Grey Plantain-eater (Crinifer zonurus), Long-crested Eagle (Lophaetus occipitalis) and Rose-ringed Parakeet (*Psittacula krameri*) in Meskebet Reservoir. The presence of these birds in Bokoro, Mai Seyie, and Meskebet reservoirs could likely be due to the presence of housing and plantations very close to the reservoirs and also the positive influence of shrub density on species richness via the provision of nesting, foraging, and roosting habitats for different bird species, for example Kites, Eagles and Vulture. Nonetheless, the presence of these birds should be interpreted with caution and only in terms of the conditions stated in this study. There could be a possibility of seeing these birds outside the study area covered here. This calls for further investigation into larger areas and/or more reservoirs than studied here. For example, Long-crested Eagle and Rose-ringed Parakeet are recorded only from Meskebet reservoir not in any of the reservoirs investigated here. However, Rose-ringed Parakeet has been recorded from Mereb river irrigation farm, which is 10 km west of Mihtsab Azmati reservoir [32]. Another surprising finding is the absence of Cape Shoveler (*Anas smithii*). A preliminary study by Asmelash et al. [23] reported the presence of Cape Shoveler in 10 reservoirs. Unfortunately, I have not seen any Cape Shoveler during the field campaigns in the 35 reservoirs, including reservoirs where it was reported to have been seen previously. This could possibly be a typical example of the local extinction of the species. Previous studies have suggested that human interference could lead to local extinction [65]. Besides, globally, 14% of the known bird species are threatened with extinction (IUCN, 2019). This clearly indicates a worrying development, and there might even be a higher risk of loss of biodiversity of aquatic birds in particular because aquatic habitats are highly sensitive ecosystems that are also threatened by global trends of climate change, agricultural expansion, and intensifications [6,66].

In conclusion, the patterns of distribution in birds are influenced by different limnological variables in the studied reservoirs. This is clearly in line with previous studies that reported that different water quality parameters such as salinity, pH and water temperature affect species richness both directly and indirectly. The direct impact of limnological parameters is that different birds have different preferences for salinity, thus affecting the presence of bird species at different salinity levels. For example, Warnock et al. [67] reported that the highest numbers and species richness of waterbirds occur at salinities around 140 and 126 ppt, respectively, in San Francisco Bay, USA. However, the effect of salinity is taxa dependent [19]. The indirect effect of limnological variables on bird species richness is that different limnological variables affect the distribution of zoobethos and aquatic animals and plants, thus affecting the use of foraging sites by waterbirds [68]. Thus, the different patterns of distribution observed in these reservoirs are possibly due to the direct and indirect effects of limnological variables. In this study, bird species richness was significantly influenced by area, which is in line with previous studies elsewhere [60]. Nevertheless, the strength of these correlations was only moderate, indicating there are other habitat variables important to species richness that were not measured in this study.

The indicator value method (IndVal analysis) has been effectively used to assign birds to high nature value (HNV) farmland and non-HNV farmland in Poland [31] and central Italy [30]. Similarly, Addisu and Girma [69] have used IndVal analysis to identify bird bioindicators in Ethiopia. The single-species approach has sometimes failed to identify species associations. This is clearly in line with previous works that suggested that a multispecies approach rather than a single-species approach is appropriate because even a few species can define more roles in bird communities and then be suitable to better characterize complex environments [30,31]. Waterbirds play key functional roles in many aquatic ecosystems and can be effective bio-indicators of change in aquatic ecosystems [70]. There is a clear consensus that waterbirds are good biological indicators, but when using waterbirds as indicators, a thorough knowledge of their ecology is essential to a monitoring program. It is my strong belief that there is a dire need for more research into the status and ecology of these essential ecosystems and their role in strengthening our knowledge of aquatic bird ecology and the natural history of African-Eurasian Migratory waterbirds. These reservoirs investigated form a gradient of many ecological variables and different degrees of eutrophication that vary with season [23] and could be excellent experimental macrocosms to study many ecological questions.

Ethics committee approval

The study complies with all regulations for ethical clearance. This study does not involve the use of human subjects (human experimentation) but involves direct field observation of vertebrates (class Aves). Permission to carry out field observation was obtained from Mekelle University, College of Natural and Computational Science, along with project registrations for VPRCS/RB/25/2012, VPRCS/RB/20/2012, and CRPO/CNCS/PhD/MU-NMBU/001/2011.

Author contribution statement

Tsegazeabe Hadush Haileselasie: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Data availability statement

Data included in article/supp. material/referenced in article.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.heliyon.2023.e17110.

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