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RESEARCH PAPER

The diversity-area relationship for waterbird communities in small artificial reservoirs over winter

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Abstract. In the middle of the 20th century, artificial reservoirs were created in Crimea due to a lack of freshwater resources. The nearest important hotspot for waterbirds is more than 100 km from these reservoirs. The five reservoirs are differently sized, and their water levels vary in response to regional climatic conditions and ice formation during winter. In this study, we investigate the bird communities of these small reservoirs using long-term waterbird surveys. Data were collected over 18 observation sessions on the five reservoirs in the winters of 2009-2021, with observations from the Simferopolske reservoirs grouped into two clusters for 2009-2014 and 2015-2021. Waterbird species richness was moderate, ranging between three and 19 species, including two considered threatened. Mallard (*Anas platyrhynchos*), Caspian gull (*Larus cachinnans*) and common gull (*Larus canus*) contributed significantly to dissimilarities between observations, with numbers of common gull decreasing significantly in relation to average January temperature and precipitation. Fisher's alpha diversity and Caspian gull number showed negative relationships with water surface area. We suggest that such negative relationships between area and diversity can be observed during cold waves when species are forced to migrate in search of more favourable conditions, leading to increased diversity in small areas.

Key words: wetlands, Crimea Peninsula, influence, water surface area, trends

Introduction

One of the most-studied and most-diverse animal communities are wetland waterbirds, i.e. species closely associated with freshwater and marine habitats. Such species are often considered indicative of ecosystem health (Shy et al. 1998, Sayagili et al. 2011) as they perform a range of ecological functions, including nutrient cycling, propagule dispersal, ecosystem engineering and biological regulation (Green & Elmberg 2014, Ogden et al. 2014, Andrade et al. 2018, Almeida et al. 2020). Waterbirds depend entirely on wetlands for activities such as foraging, resting and moulting (Debela et al. 2020). Numerous recent studies examining waterfowl populations in wetlands ecosystems have demonstrated that wetlands are disappearing faster than many other landscape types and are becoming one of the most endangered ecosystems worldwide (Benassi et al. 2007, Šťasný & Riegert 2021). A 17-19% decline in overall breeding bird abundance in Europe since 1980 (Burns et al. 2021) is likely a consequence of similar decreases in the area of breeding habitat, whether wetland or dry. Winter is a critical period for wetland birds, as they are exposed to extreme temperature fluctuations, food shortages and increased anthropogenic pressure. Furthermore, climate change will likely affect wintering birds more than breeding populations (Lehikoinen et al. 2021). Recent declines in many European bird species have been linked to environmental change, especially those related to land use and climate (Bowler et al. 2021). Indeed, while multiple factors influence species-diversity patterns, the climate is now amongst the most important (Riberio et al. 2019), with local environmental changes, such as increasing/decreasing precipitation and temperatures, likely to lead to shifts in breeding, migration and overwintering areas in many species. According to Marchowski et al. (2018) and Rosenberg et al. (2019), birds can be considered reliable indicators of such changes.

The Crimean Peninsula, located in the northern part of the Black Sea (Fig. 1), has an area of about 26,000 km^2 and is unevenly divided into two parts, a mountain-forest area of 6,000 km^2 and a plain area of around 2,000 km^2. Over 320 bird species have been recorded in the country (e.g. Kostin 1983, Prokopenko et al. 2012, Kucherenko et al. 2017b), and millions use the peninsula as migration and overwintering stopovers, many of which are of global and local importance (Kostin 1983, Akimov & Radchenko 2009, Ivanov et al. 2015, Andruyshchenko et al. 2019, Kucherenko et al. 2020). Most of these sites are concentrated in Natural Reserves, 12 important bird areas (Dudkin 2003) and six Ramsar wetlands (Ramsar sites information services 2022, https://www.ramsar.org/wetland/ukraine). While the Eastern and Central Syvash Ramsar wetlands, located on Syvash Bay and the Azov Sea, respectively, are the most important sites for wintering waterbirds in the country, the Azov-Black Sea region of Ukraine has many large wetlands areas maintaining numerous waterbirds. These sites have low water levels and provide vast food resources and a wide range of shelter types, including remote islands and peninsulas, bays and cays rarely visited by humans. Furthermore, owing to a predominance of relatively warm weather and little snow, most of these wetlands (or parts of them) and coasts are only covered with ice or snow for a short period. Consequently, most waterbirds have a plentiful food supply during the winter and regularly stay in the region (Andruyshchenko et al. 2015). Six Ramsar wetlands are in this area (Ramsar sites information services 2022, https://www.ramsar.org/wetland/ukraine). However, the Eastern and Central Syvash are most important for wintering waterbirds (Marushevsky et al. 2005). In contrast to the littoral zone and bays of the Azov-Black Sea, the inland region of Crimea (a peninsula in the northern part of the Black Sea) has relatively few freshwater wetlands, though there were small mountain rivers and freshwater sections in the salt lakes of lowland Crimea in the past. In the middle of the 20th century, however, a series of reservoirs were constructed to counter this lack of freshwater, most of which were formed by building a dam on the largest mountain river flows, e.g. Simferopolske on the River Salhyr, Partyzanske on the River Alma and Bilohirs'ke on the River Biyuk-Karasu. This situation led to water accumulation upstream of the dam and the subsequent appearance of suitable habitat for a range of species, including waterbirds (Podgorodetsky 1988, Oliferov & Timchenko 2005, Kucherenko & Chirniy 2011, Kucherenko et al. 2015). Since then, reservoir modifications have affected different ecological bird taxa, both terrestrial and waterfowl (Jones et al. 2016, Irving et al. 2018). Before the construction of the reservoirs, there were no wetlands in the mountainous part of the peninsula; thus, aquatic birds either had to migrate across the region or were only recorded sporadically. For example, Eastern Syvash, the nearest important hotspot for birds, especially in winter, is located more than 100 km from the reservoirs, while the closest distance to the sea coast from the reservoirs is from 30 to 50 km. Many studies have examined bird diversity and ecology along the Ukrainian Azov-Black Sea coast and Crimea (Andruyshchenko et al. 2015, 2019, Kucherenko & Kalinovsky 2018, Kucherenko et al. 2020). These have highlighted the significance of wetlands for different species in terms of phenology, dynamics and distribution (e.g. Kucherenko & Chirniy 2011, Kucherenko et al. 2015, 2017a). Immigration, one of the processes in the island biogeography equation, is well documented in Crimean avifauna (Prokopenko et al. 2012, Tsvelykh & Kucherenko 2020), including aquatic species (Vergeles et al. 2012, Kucherenko et al. 2015, 2017b, 2018); however, such studies tend to concentrate on nesting species. Nevertheless, all phenological periods are important for monitoring bird activity, and data from all seasons are required to fully assess the significance of a locality for bird maintenance during winter (Kwieciński et al. 2016, Morelli et al. 2018). Data on the diversity of waterbirds in isolated reservoirs, especially in winter, are relatively rare in the literature, and studies of waterbirds tend to be more common from Ramsar wetlands and other hotspots than small ponds. Consequently, this study aimed to investigate bird communities at five reservoirs located some distance from such hotspots using long-term waterbird surveys. Furthermore, as winter is a critical period in the lives of birds, we began our observations during this season.

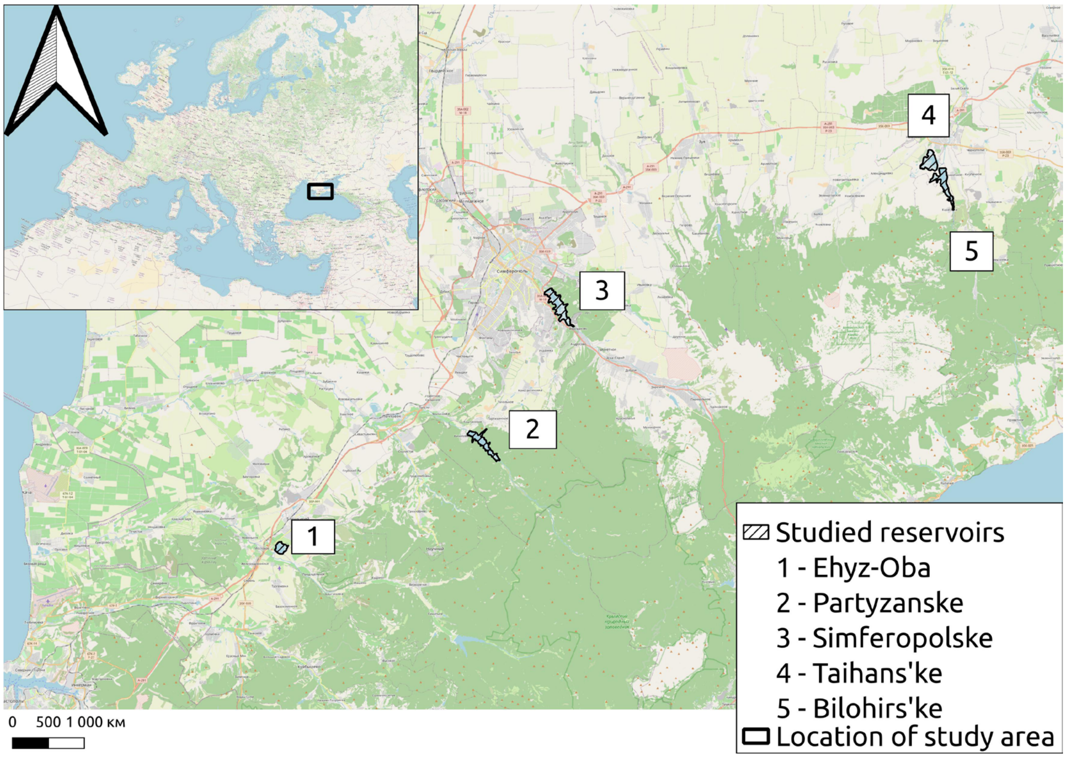

Fig. 1. Map of the study area. The green area represents woodland and forest in the mountain-forest zone of the Crimean Peninsula.

Material and Methods

Study area

Five model reservoirs in the mountainous region of Crimea were selected for this investigation (Fig. 1). The Ehyz-Oba reservoir (near the town of Bakhchisarai) is surrounded by arable fields, artificial forests, roads and settlements; the Partyzanske reservoir (south-west of Simferopol city) lies between a forest and a settlement in the north; the Simferopolske reservoir (south of Simferopol city) is surrounded by settlements to the west and an artificial forest to the east; and the Bilohirs'ke and Taihans'ke reservoirs (east of the town of Bilohirsk) are located side by side among arable fields and settlements. The reservoirs are all between 300 and 400 m above sea level, surrounded by predominantly forested habitats (Kucherenko & Ivanovskaya 2020), with some open grassland areas and arable fields, and all are located close to residential areas and roads. None of the wetlands investigated have aquatic vegetation.

Of the 18 observation sessions completed, 11 were carried out at the Simferopolske reservoir, with four other reservoirs studied additionally in some years to extend the geographic representativeness. The reservoirs have variable hydroperiods, depending on regional climatic conditions and wide fluctuations in water volume. During the winter, the free-water surface area is reduced due to ice, which can cover 50-70% of the water surface. However, the coldest part of winter is relatively short, and complete freezing of the water surface rarely occurs. Overall, the average area of the water surface ranges from 39 to 275 ha (median = 120.0 ha) and, in most cases, the decrease in water level is due to ice cover. In Simferopolske reservoir, the average maximum temperature in January ranges between 2.6 and 6.0 °C (mean 4.8 °C), with a minimum temperature ranging from –1.8 to 0.1 °C (mean –1.2 °C) and precipitation ranging from 44.6 to 94.3 mm (67.5 mm) per year. The reservoirs, which are all situated on rivers fed by atmospheric precipitation, have volumes ranging from 6.89 million m^3 (Ehyz-Oba) to 36 million m^3 (Simferopolske) and depths ranging from 16 m (Ehyz-Oba, Taihans'ke) to 40 m (Partyzanske) (Oliferov & Timchenko 2005). As the water surface area changes regularly, we calculated the water surface area of each reservoir using Landsat-5, Landsat-8 and Sentinel-2 satellite images downloaded from an open Internet source (United States geological survey 2021, https://earthexplorer.usgs.gov/) taken on the closest date to the bird counts. Cloud cover was also considered (usually less than 10%). As no suitable images were available for 2012, data for this year were excluded from some analyses. The distance of each reservoir from Eastern Syvash, i.e. the nearest waterbird hotspot, was also calculated as a measure of the reservoir's isolation. Finally, the average maximum temperature and precipitation in January 2010-2018 (Harris et al. 2014, Fick & Hijmans 2017) were used to assess their influence on bird overwintering.

Bird survey

As the reservoirs surveyed all have a relatively small area and smooth banks, we used the 'complete counting method' (Bibby et al. 2000, Sutherland 2006). Birds were observed from dawn to noon in late January and early February by walking along the wetland coast and counting all birds present, always choosing a day without precipitation. At larger reservoirs, the areas were divided into non-overlapping sectors and the birds were counted in each sector. Each survey lasted one to four hours, depending on the reservoir size. Birds were identified and counted using a pair of 10 × 40 binoculars and a 20 × 50 telescope. As we were specifically investigating wetland diversity, we limited our analyses to obligate wetland users from the overall avian fauna present (Weller 1999), i.e. the orders Podicipediformes, Pelecaniformes, Ciconiiformes, Anseriformes, Falconiformes (with a single species, white-tailed eagle, *Haliaeetus albicilla*), Gruiformes, Charadriiformes and Coraciiformes (with a single species, kingfisher, *Alcedo atthis*). We then calculated the following diversity representations: species richness at a single reservoir, number of individuals, the Shannon index and Fisher's alpha diversity, which describe the number of species and number of individuals of that species, thereby providing an informative and robust diversity measure (Fisher et al. 1943, Magurran 2004). Using such diversity-area relationships extends the species-area relationship law for biodiversity and biogeography analysis (Ma 2018).

Statistical analysis

All data analysis was carried out using R statistical software version 4.2.1 (R Development Core Team 2022). Non-metric multidimensional scaling (NMDS), provided in the R "vegan" package (Oksanen et al. 2022), was used to compare changes in the waterbird community at the Simferopolske Reservoir, while the SIMPER function in the "vegan" package was used to measure the percentage contribution of each species in a Bray-Curtis dissimilarity matrix (Clarke 1993). The "dist" function, with Euclidean distance, and the "hclust" function, based on the Wald method, were used to apply community clustering. A linear regression model, estimated using ordinary least squares regression, was fitted to evaluate the relationships between different characteristics of species diversity (i.e. species richness, total number of individuals, number of individuals of each species, Fisher's alpha diversity and the Shannon index), distance from the reservoir to the Eastern Syvash, water surface area of each reservoir and reservoir volume. This model was used to identify explanatory variables related to response variables, describe the form of the relationships, and provide an equation for predicting the response variable from the explanatory variable (Kabacoff 2011). The assumptions of linear regression (Zuur et al. 2007, Kabacoff 2011) and model validation were then checked using the "car" and "gvlma" packages (Kabacoff 2011, Fox & Weisberg 2019, Pena & Slate 2019). The Shapiro-Wilk normality test was applied to check the normality of variables and regression residuals, with dependent and independent variables normalised by converting to a natural logarithmic scale when necessary and data +1 applied in the case of zero. The Mann-Whitney test was used to compare outcomes between two groups. Standardised parameters were obtained by fitting the model to a standardised version of the dataset, with 95% confidence intervals (CIs) and P values computed using the Wald approximation. The diversity indices were then calculated using the "vegan" package (Oksanen et al. 2022). The model was selected by manipulating the number of independent variables, with the best model chosen based on the lowest Akaike information criterion (AIC; Akaike 1998) and a significant ANOVA test (James et al. 2021) after dropping explanatory variables one by one. We then chose the model with the most significant explanatory variables ($P < 0.05$) to describe the relationship. When the fitted model had both significant and non-significant variables, we removed the non-significant values, rechecked the AIC and chose the lowest result. To evaluate the influence of average maximum temperature and precipitation in January on the number of individuals of each species, we used observations from the Simferopolske reservoir only as data collected over the longest period. Based on this data, we assessed any trends in numbers using Poisson generalised linear models (GLM), with standard errors corrected using a quasi-GLM model (Zuur et al. 2009) in cases of overdispersion. The "ggplot2" package was then used to visualise any relationship between dependent and independent covariance (Wickham 2016). Coverage of the study area and open water surface area at each wetland was calculated (in ha) using QGIS version 3.26.0 (QGIS Development Team 2022).

Table 1. Species composition, mean number (X), standard deviation (SD) and dominance (D) of birds overwintering on five Crimean reservoirs between 2009 and 2020. Note: X abs = total number of individuals per reservoir.

Species	Ehyz-Oba		Partyzanske		Simferopolske		Taihans'ke		Bilohirs'ke		Total	
	X ± SD	D (%)	X ± SD	D (%)	X ± SD	D (%)	X abs	D (%)	X abs	D (%)	X ± SD	D (%)
Cygnus olor	1.5 ± 2.1	0.1	0	0	0	0	0	0	2	0.4	0.3 ± 0.8	0.1
Cygnus cygnus	0	0	0	0	0.1 ± 0.3	0.1	0	0	0	0	0.06 ± 0.2	0.1
Anser albifrons			0.3 ± 0.6	0.1	0	0	0	0	0	0	0.06 ± 0.2	0.1
Tadorna tadorna	0	0	0.3 ± 0.6	0.1	1.5 ± 3.4	0.1	0	0	0	0	0.9 ± 2.7	0.1
Tadorna ferruginea	0	0	0	0	0.1 ± 0.3	0.1	0	0	0	0	0.06 ± 0.2	0.1
Anas plathyrhynchos	267.0 ± 245	24.7	1,287.3 ± 2,047.0	93.4	463.5 ± 607.0	45.8	0	0	400	84.0	549.7 ± 917.7	53.2
Anas acuta	0	0	1.7 ± 2.9	0.1	0.7 ± 2.4	0.1	0	0	0	0	0.72 ± 2.2	0.1
Anas penelope	0	0	6.7 ± 11.5	0.5	3.0 ± 6.7	0.2	0	0	0	0	2.9 ± 6.8	0.1
Anas crecca	140.0 ± 99.0	12.9	58.7 ± 79.7	4.3	80.6 ± 177.0	7.5	0	0	0	0	74.6 ± 144.8	7.2
Aythya ferina	87.5 ± 44.5	8.1	2.7 ± 4.62	0.2	33.8 ± 93.8	3.1	0	0	0	0	30.8 ± 77.0	3.0
Netta rufina	12.5 ± 16.3	1.2	0	0	0.4 ± 0.8	0.1	0	0	0	0	1.6 ± 5.6	0.2
Aythya fuligula	3.5 ± 5.0	0.3	2.7 ± 1.2	0.2	6.7 ± 9.6	0.6	0	0	44	9.2	7.4 ± 12.0	0.7
Bucephala clangula	0	0	0	0	1.3 ± 2.3	0.1	0	0	0	0	0.8 ± 1.9	0.1
Mergus serrator	0	0	0	0	0.2 ± 0.6	0.1	0	0	0	0	0.1 ± 0.5	0.1
Oxyura leucocephala	0	0	0	0	0.1 ± 0.3	0.1	0	0	0	0	0.06 ± 0.2	0.1
Gavia arctica	0	0	0	0	0.2 ± 0.6	0.1	0	0	0	0	0.1 ± 0.5	0.1
Podiceps nigricollis	0	0	0.7 ± 0.6	0.1	18.5 ± 17.9	1.7	0	0	0	0	11.4 ± 16.5	1.1
Tachybaptus ruficollis	0	0	0	0	0.6 ± 2.1	0.1	0	0	0	0	0.4 ± 1.7	0.1
Podiceps cristatus	0	0	2.3 ± 4.1	0.2	9.9 ± 15.2	0.9	0	0	4	0.8	6.7 ± 12.5	0.6
Phalacrocorax carbo	0	0	1.3 ± 1.5	0.1	4.9 ± 8.4	0.5	0	0	26	5.5	4.7 ± 8.7	0.5
Egreta alba	0.5 ± 0.7	0.1	0.7 ± 0.6	0.1	2.3 ± 2.9	0.2	0	0	0	0	1.6 ± 2.4	0.2
Ardea cinerea	0.5 ± 0.7	0.1	0	0	1.6 ± 2.7	0.2	1	20	0	0	1.1 ± 2.2	0.1
Haliaeetus albicilla	0	0	0.3 ± 0.6	0.1	0.4 ± 0.9	0.1	2	40	0	0	0.4 ± 0.8	0.1
Fulica atra	567.0 ± 612.4	52.4	12.7 ± 21.9	0.9	99.8 ± 123.1	9.2	0	0	0	0	126.1 ± 241.9	12.2
Calidris alpina	0	0	0	0	0.1 ± 0.4	0	0	0	0	0	0.06 ± 0.2	0.1
Chroicocephalus ridibundus	0	0	0	0	0.5 ± 0.8	0.1	0	0	0	0	0.3 ± 0.7	0.1
Larus canus	1.0 ± 1.4	0.1	0	0	130.9 ± 274.5	9.6	0	0	0	0	80.1 ± 220.5	7.7
Larus cachinnans	0.5 ± 0.7	0.1	0.7 ± 0.6	0	214.0 ± 272.4	20.0	2	40	0	0	131.1 ± 234.7	12.6
Hydrocoloeus minutus	0	0	0	0	0.2 ± 0.4	0.1	0	0	0	0	0.1 ± 0.3	0.1
Alcedo attis	0	0	0	0	0.1 ± 0.3	0.1	0	0	0	0	0.06 ± 0.2	0.1

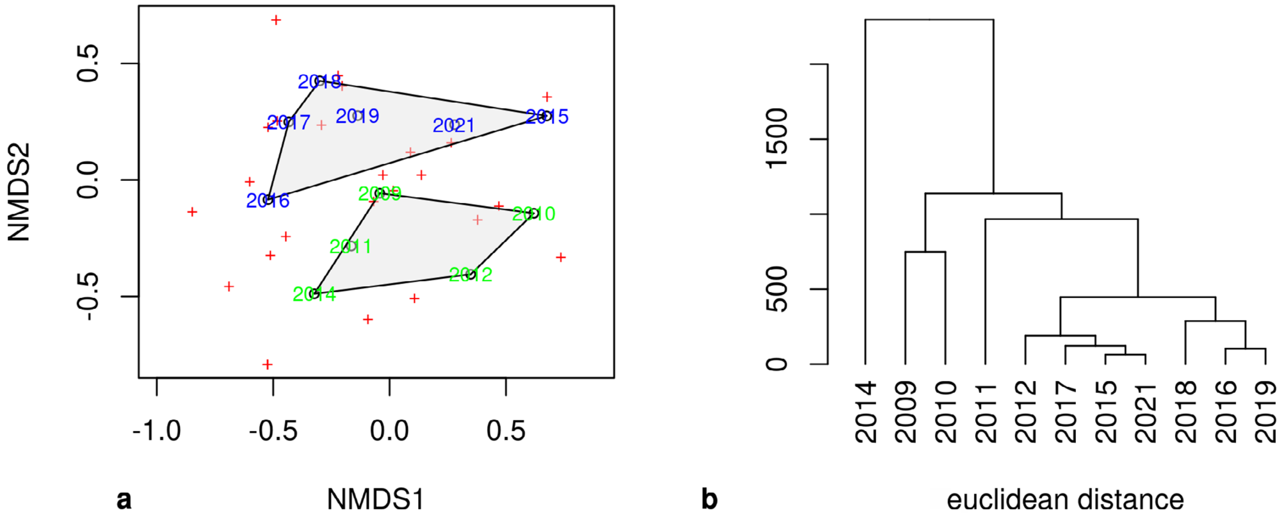

Fig. 2. Results of a) nonmetric multidimensional scaling (NMDS) and b) clustering based on the Wald method, showing dissimilarity between the overwintering waterbird community at Simferopolske reservoir between 2009 and 2021.

Results

In total, 18,614 individuals of 30 wetland bird species were recorded, the most abundant being mallard (53.2% of total number of individuals), Caspian gull (12.6%), and Eurasian coot (*Fulica atra*; 12.2%) (Table 1). The mallards and Eurasian coots were obligate visitors to all reservoirs and fed there, while the gulls tended to drink and rest at the reservoir but feed on the city landfill site (located 5 km north-east). Two species recorded were included in the IUCN Red List of Threatened Species, i.e. common pochard (*Aythya farina*; classed as vulnerable) and white-headed duck (*Oxyura leucocephala*; vulnerable). The white-tailed eagle was also observed, which was only assessed for the IUCN Red List of Threatened Species in 2021. While the common pochard is a regular winter visitor, white-tailed eagles winter only occasionally and white-headed ducks have been recorded only once. The number of individuals per water body ranged widely from five to 3,887 (median = 734 ind.). The largest number of species was detected at Simferopolske reservoir in 2014 (19), while the largest number of individuals was recorded at Partyzanske (3,887) the same year. The lowest number of birds (five individuals of three species) was recorded at the Taihans'ke reservoir in 2015.

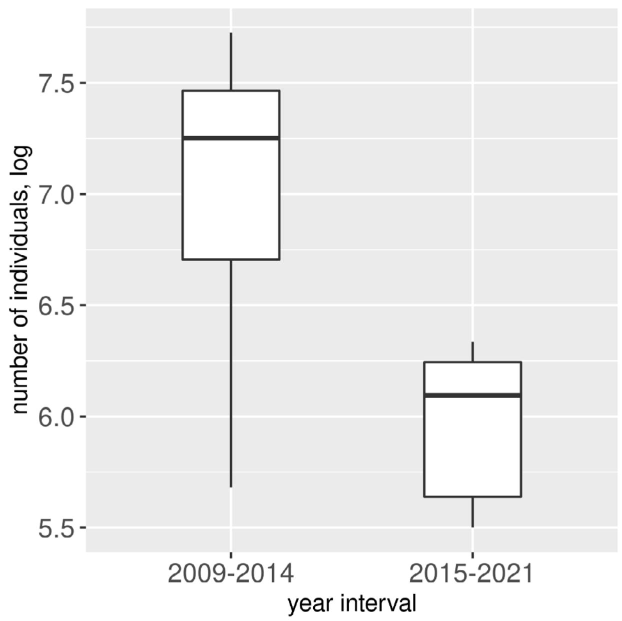

Fig. 3. Differences in the sum of common mallard (*Anas plathyrhynchos*), common gull (*Larus canus*) and Caspian gull (*L. cachinnans*) at the Simferopolske reservoir between 2009 and 2021. The boxplot shows the median and 25th and 75th percentiles; the whiskers indicate the value within 1.5 times the interquartile range.

Between 2009 and 2021, the bird community at Simferopolske often changed, with the number of species observed ranging from six in 2015 to 19 in 2014 (median = 10) per observation. The number of individuals per observation followed the same trend, varying from 302 individuals in 2015 to 3,354 in 2014 (median = 753), with the most abundant species being mallard (45.8%), Caspian gull (20.0%), common gull (9.6%), Eurasian coot (9.2%) and Eurasian teal (*Anas crecca*; 7.5%). The NMDS ordination indicated that the observations were grouped into two clusters, i.e. 2009-2014 and 2015-2021 (Fig. 2), while SIMPER showed that three species contributed significantly to dissimilarities between observations, i.e. mallard, Caspian gull and common gull. Though the number of individuals of each species in 2009-2014 differed from 2015-2021, these differences were not significant (Mann-Whitney test, $P > 0.05$); however, the sum of individuals of these species differed significantly (Mann-Whitney test, $P < 0.05$; Fig. 3), suggesting

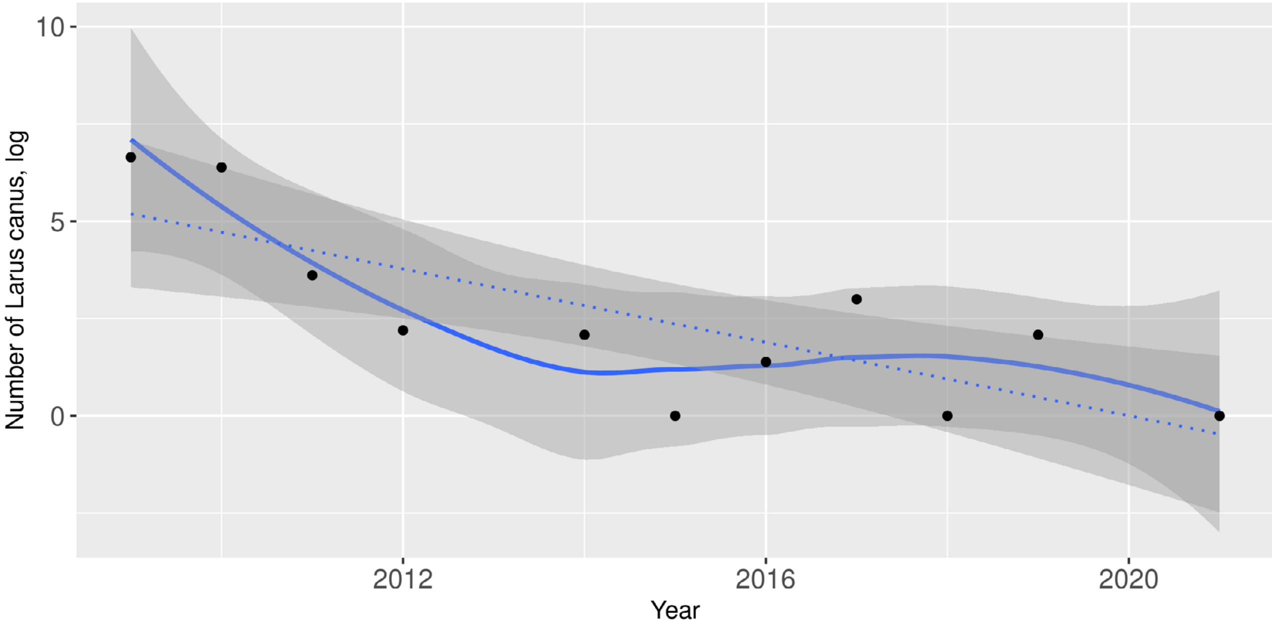

Fig. 4. Scatterplot of common gull (*Larus canus*) numbers (logarithmic scale) by year at the Simferopolske reservoir between 2009 and 2021, fitted with linear (dotted line) and smoothed regressions.

Table 2. Results of a quasi-GLM model to assess the influence of environmental parameters and trends on common gull (*Larus canus*) numbers at the Simferopolske reservoir between 2009 and 2021, with water area, min and max temperature, precipitation and number trends (year) as response variables.

	Estimate	Std. Error	t-Value	Pr (>|t|)
(intercept)	980.0	169.3	5.8	0.03
Max temperature	–1.3	0.2	–5.7	0.03
Trends	–0.5	0.1	–5.8	0.03

Table 3. Results of a linear model to assess the influence of water area on Fisher's alpha diversity, with logarithm of water area (ha) and its quadric term as response variables.

	Estimate	Std. Error	t-Value	Pr (>|t|)
(intercept)	16.784	4.617	3.64	0.003
Area (ha, log)	–7.055	1.99	–3.54	0.003
Quadric term of area (ha, log)	0.747	0.211	3.53	0.003

these three species influenced the general trend of community grouping. Clustering based on the Wald method confirmed that observations in 2014 were the most distinctive (Fig. 2), the same year when the highest number of birds was registered on the reservoir. Another cluster grouped numbers of individuals

Table 4. Results of a linear model to assess the influence of water area on Caspian gull (*Larus cachinnans*) numbers, with logarithm of water area (ha) and its quadric term as response variables.

	Estimate	Std. Error	t-Value	Pr (>|t|)
(intercept)	71.833	26.055	2.76	0.015
Area (ha, log)	–32.016	11.232	–2.85	0.013
Quadric term of area, (ha, log)	3.619	1.193	3.03	0.009

in 2009 and 2011 (1,844 and 1,565, respectively). The numbers of common gulls demonstrated a significant negative trend between 2009 and 2021 (Fig. 4), with a quasi-GLM indicating the species was significantly affected by water surface area, average maximum January temperature and precipitation (formula: number of common gull ~ area + January average maximum temperature + precipitation + Year(trend)) (Table 2), the model's explanatory power being highly significant (Nagelkerke's R^2 = 1.00, t(2) = 5.79, $P < 0.001$). The influence of environmental parameters on other species and trends in numbers at the Simferopolske reservoir were non-significant.

The predictors used in the regression model did not affect species richness, overall number of individuals of all species, numbers of most single species or Shannon's diversity indices. The best result was obtained when we fitted Fisher's alpha diversity

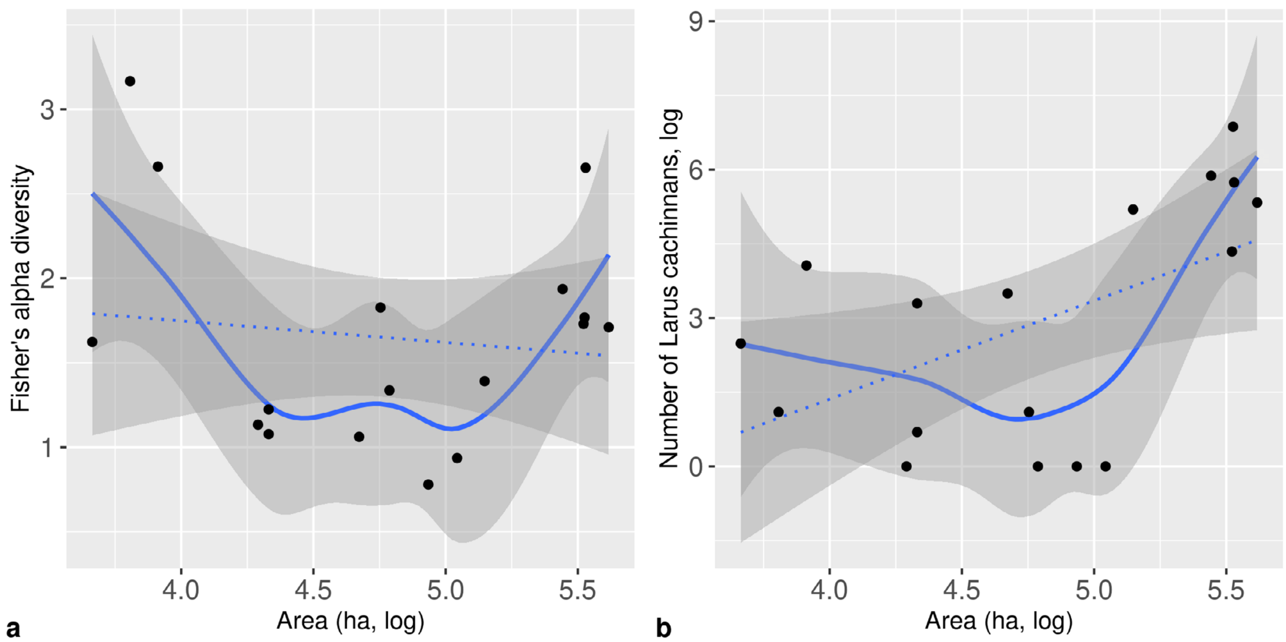

Fig. 5. a) Scatterplots of Fisher's alpha diversity by area (logarithmic scale), and b) the number of Caspian gulls (*Larus cachinnans*) by area (logarithmic scale), fitted with linear (dotted line) and smoothed regressions.

and numbers of Caspian gulls with the linear model (estimated using ordinary least squares regression) to predict Fisher's alpha diversity with an area (formula: log(Fisher's alpha diversity) ~ log(area, ha) + quadric term (log(area, ha)) explaining a significant proportion of variance ($R^2 = 0.47$, $F_{2, 14} = 6.29$, $P = 0.011$, adj. $R^2 = 0.40$; Table 3). The impact of distance to Eastern Syvash and volume appeared to be non-significant as the AIC value increased; consequently, we extracted this parameter from the resulting model. The relationship between the diversity index and water surface area proved negative (Fig. 5, Table 4), as did the number of Caspian gulls with water surface area. The model also explained a significant proportion of variance ($R^2 = 0.57$, $F_{2, 14} = 9.16$, $P = 0.003$, adj. $R^2 = 0.50$; Fig. 5, Table 4). No other species showed a significant relationship with surface area. Distance to Eastern Syvash, the main stopover site for waterfowl, and reservoir volume also proved non-significant. The significance of quadric terms for both models increased the model fit and suggested two relationship patterns, i.e. a negative relationship in the case of small water areas, which then became a positive relationship when the water surface area reached 5.0 (Fig. 4).

Discussion

All the reservoirs surveyed in this study were small, deep freshwater bodies; consequently, waterbird species diversity was moderate. Nevertheless, species richness at some of the waterbodies was comparable with that at the nearest waterbird hotspot, Eastern Syvash, where 9-20 species were recorded during International Waterbird Census counting undertaken between 2011 and 2017 (Kostiushyn & Andryushchenko 2017). The list of dominant species at this site was also similar, with mallard, Eurasian coot, and Caspian and common gulls dominant; however, there were more species with higher numbers in Eastern Syvash. For example, white-fronted goose (*Anas albifrons*) and shelduck (*Tadorna tadorna*) were numerous in Eastern Syvash but rarely recorded in our reservoirs. On the other hand, the Eurasian teal was one of the more abundant species in our study (ca. 8% of the total number; Table 1) but only occurred occasionally at Eastern Syvash. Between 2008 and 2011, the dominant species in the southern coastal wetlands of Crimea differed from that in the study reservoirs, being comprised mainly of Eurasian coot, black-headed gulls (*Chroicocephalus ridibundus*), greater cormorant (*Phalacrocorax carbo*) (Beskaravayny 2008) and grebes, including the black-necked grebe (*Podiceps nigricollis*), great crested grebe (*Podiceps cristatus*) and little grebe (*Tachybaptus ruficollis*) (Ciach 2011). Thus, despite belonging to the same wintering range, the distribution of different waterbird species differed significantly with biotopes. Overall, species richness and diversity in the study reservoirs were less than that in small Mediterranean reservoirs, where more than 100 species have been observed, at greater numbers, in ponds ranging between 2 and 1,007 ha (Carvalho et al. 2013, Giosa et al. 2018). Likewise, more species were recorded overwintering in the Czech Republic between 2009 and, where 79 waterbird species have been observed (Musilová et al. 2014). On the other hand, the Crimean reservoirs demonstrated higher species richness than Turkish lakes in winter, where between 11 and 26 species have been registered on waterbodies ranging from 900 to 26,000 ha (Sayagili et al. 2011). Generally speaking, dabbling ducks were more abundant in the study wetlands than diving ducks, a similar trend to that observed for overwintering waterbirds in the Mediterranean and Central Europe. The presence of the two vulnerable species at our sites suggests that they are moderately important wintering sites, but their importance could increase in the case of climate deterioration.

Changes in species richness and number of individuals are relatively common in the Azov-Black Sea wintering waterbird community, even over one winter (Andruyshchenko et al. 2015). Our study recorded the highest species richness and number of individuals per reservoir in 2014, though only at Simferopolske and Partyzanske. While both these reservoirs have a large water surface area compared to the other ponds, there are other reasons. Throughout the 11-year observation period, the highest number of birds recorded at Simferopolske occurred in 2014. Satellite images for this period show a lot of snow and ice over a large area, forcing waterfowl to concentrate at ice-free sites. Conversely, the lowest species richness and number of individuals was recorded the following year, 2015, with 302 individuals from six species. This decrease appeared to be associated with a complete absence of diving ducks (i.e. common pochard, tufted duck (*Aythya fuligula*)), diving fishers (black-necked grebe, great crested grebe) and common gulls, despite diving ducks and fishers being recorded in almost all other observation years. That same year (2015), we did observe diving ducks and diving fishers in wetlands located outside the study reservoirs, i.e. in the Sevastopol Bays (south-west of Crimea) and Donuzlav Lake (north-west of Crimea). This observation suggests that the reservoirs, unlike other Crimean wetlands, are not always used by such species (Ciach 2011, Andruyshchenko et al. 2015), possibly due to a shifting of wintering areas in response to global climate change or local ecological situations. Indeed, a shift of wintering waterbird areas from north-west Europe to the north-east has already been demonstrated in European populations (Lehikoinen et al. 2013, Marchowski et al. 2018). While the abundance of several species appeared to decrease at Simferopolske over the observation period, only the number of common gulls decreased significantly. Unfortunately, we could not find reliable population trends for common gulls worldwide (Birdlife Data Zone 2023, http://datazone.birdlife.org/species/search). Pavón-Jordán et al. (2020) have suggested that changing temperatures could have a positive impact on wintering waterbirds in Europe and North Africa; however, in our study, we observed no significant influence of rising temperatures or precipitation on any species, except for a negative influence on the number of common gulls (Table 2). The lack of influence on other species may have been because such processes do not occur at a local level and so are not detected, or local studies require longer observation periods.

Numerous publications have examined the relationship between species diversity and 'habitat' area, whether it be for woody plants or different classes of animals, such as insects, molluscs, mammals or birds, and most have found that larger areas contain higher species richness (MacArthur & Wilson 1963, Brown 1981, Coleman et al. 1982). In our study, however, we found a negative relationship between water surface area and two independent variables, Fisher's alpha diversity and Caspian gull number, all other diversity indices being non-significant. While Shannon's index is generally used more often than Fisher's index for such studies, it is nevertheless a robust measure of diversity (Magurran 2004). In comparison, while there was no significant influence of wetland volume or distance to the nearest waterbird hotspot in Mediterranean wetlands, water volume significantly impacted species richness and diversity (Giosa et al. 2018).

Conditions at the nearest waterbird hotspot, Eastern Syvash, may have affected the number of wintering waterbirds in the nearby wetlands. The Eastern Syvash wetland is relatively shallow, at about 1 m deep; thus, in cold snaps, it readily freezes over. In comparison, the reservoirs are deeper, at up to 40 m; hence they tend to have ice-free patches for longer. During the freeze period, ice may cover the main wintering stopover site more rapidly than at the deeper reservoirs, forcing the birds to fly to other sites in search of suitable ecological conditions, causing the diversity of waterbirds at the reservoirs to increase as new individuals arrive. While the water surface at the reservoirs also decreases, the remaining open-water sites will continue to attract birds. In support of our assumption, researchers collecting data on the southern Crimean coast noted an increase in bird numbers during freezing weather, especially after abrupt decreases in temperature (Pusanow 1933, Beskaravayny 2008). Our observations suggest that a negative relationship between area and diversity may be observed during cold snaps when species are forced to migrate in search of more favourable conditions, though this may also lead to an increase in diversity on smaller open waterbodies. A similar pattern has been described in Slovakia, where ice cover had a positive effect on the total abundance of all waterbird species and the numbers of some abundant species at river sites (Urban et al. 2021); the authors suggest it was caused by waterbirds moving to river sites when still waters became frozen. This negative relationship may also be caused by non-resident wintering bird species, which may be more capable of moving rapidly in response to changing ecological conditions. Alternatively, this disagreement with theory may indicate that the reservoirs we examined cannot be considered as true 'islands' but rather as island-like anthropogenically-fragmented habitat systems (Itescu 2019).

Data Availability Statements

The data supporting this study are available in Zenodo, the open-access repository, https://doi.org/10.5281/zenodo.7015526.

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