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Articles

Key factors of avian diversity and sustainability in the forest-steppe lakes of Western Siberia

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Key factors of avian diversity and sustainability in the forest-steppe lakes of Western Siberia

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Abstract

The article examines the relationship between various parameters of 25 forest–steppe lakes in Western Siberia and the biological diversity of bird communities, based on bird censuses conducted from 2002 to 2023. It focuses on factors such as the lakes' physical characteristics, climate zone peculiarities, salinity levels, lake area, and the extent of overgrowth. A total of 180 bird species typical of the Western Siberia forest–steppe zone were recorded. The study found a statistically significant differentiation in bird communities across subzones, with the mean total bird abundance in the middle forest–steppe being 2.5 times greater than that in the northern forest–steppe. Correlation analysis revealed a significant inverse relationship between lake salinity levels and both species number and total bird abundance, as well as the species diversity and resilient sustainability indices of water bird communities. Conversely, a significant direct influence of salinity on the resistant sustainability index was observed. Additionally, a statistically significant, albeit weak, positive correlation was found between total bird abundance and the degree of lake overgrowth by aquatic and semi-aquatic vegetation. However, no clear correlation was established between the area of the lakes and the examined properties of bird communities.

Keywords

Biodiversity, bird community, community sustainability, indices, forest–steppe zone, Western Siberia, wetland areas

Introduction

Over the 20th and 21st centuries, the environment of Western Siberia has experienced significant changes, primarily driven by human economic activities and climate change (Gashev et al. 2017). Key human-induced factors affecting the forest-steppe ecosystems of Western Siberia include the farming industry, urbanization, wildfires, and extensive deforestation (Kuranov 2008; Vetluzhskikh 2013; Brinkert et al. 2016; Kämpf et al. 2016; Lupinos et al. 2017). For instance, a comprehensive assessment of biodiversity in the Western Siberia forest-steppe and its relationship with climate change reveals a notable inverse correlation between the abandonment of agricultural lands and the diversity of plant, insect, mammal, and bird species (Wertebach et al. 2017; Kamp et al. 2018). Some studies indicate that these factors have both direct and indirect effects on ecosystems. However, the impact of specific biotic and abiotic factors on the diversity and sustainability of bird communities remains insufficiently explored (Gawlik 2002; Chopra and Adhikari 2004; Xia et al. 2010; Wen et al. 2011; Katayama et al. 2014; Zhang et al. 2015; Chen et al. 2016; Chastant and Gawlik 2018; Senner et al. 2018; Levykh and Boldyrev 2018; Gao et al. 2020; Bai et al. 2021; Boldyrev et al. 2021; Wang et al. 2022; Zou et al. 2021). Wetland ecosystems, in particular, are notably understudied in this context (Frederick and Ogden 2001; Reid et al. 2013; Zhao et al. 2018; Giese et al. 2018; Wang et al. 2019; Tyulkin 2022).

Previous research on the wetland areas of the Western Siberia forest-steppe zone has focused on wintering bird gatherings, documented migratory species during seasonal migrations, and, to a lesser extent, examined the factors influencing the formation and functioning of these communities (Azarov 1984; Blinova and Blinov 1999; Yakimenko 2007; Lupinos et al. 2016; Lupinos et al. 2017; Soloviev and Vartapetov 2021; 2023). These considerations underscore the need for further research, which aims to investigate the diversity and sustainability of bird communities inhabiting the forest-steppe lakes of southern Western Siberia, as well as the factors shaping these communities.

Materials and methods

In the field seasons of 2002, 2012, 2015–2017, and 2019–2023, the avifauna of Western Siberia's lakes was studied across six districts in Kurgan Oblast (including Kurgan urban okrug and the Belozersky, Ketovsky, Lebyazhevsky, Makushinsky, and Mokrousovsky districts) and eight districts in Tyumen Oblast (comprising Abatsky, Armizonsky, Berdyuzhsky, Isetsky, Ishimsky, Kazansky, Sladkovsky, and Vikulovsky districts) in Russia. The research focused on twenty-five lakes situated in two geographical subzones: northern and middle forest–steppe (see Fig. 1). Most of these lakes are part of the unique natural region known as the Tobol–Ishim forest–steppe, located within the Tobol–Ishim interfluve. This wetland area, recognized as a Ramsar site of international significance, serves as a vital breeding ground for various aquatic and semi-aquatic bird species and is positioned along one of the major migratory flyways. The region's favorable combination of climate, landscape, and hydrological conditions creates unique habitats that support birds during both their breeding seasons and seasonal migrations.

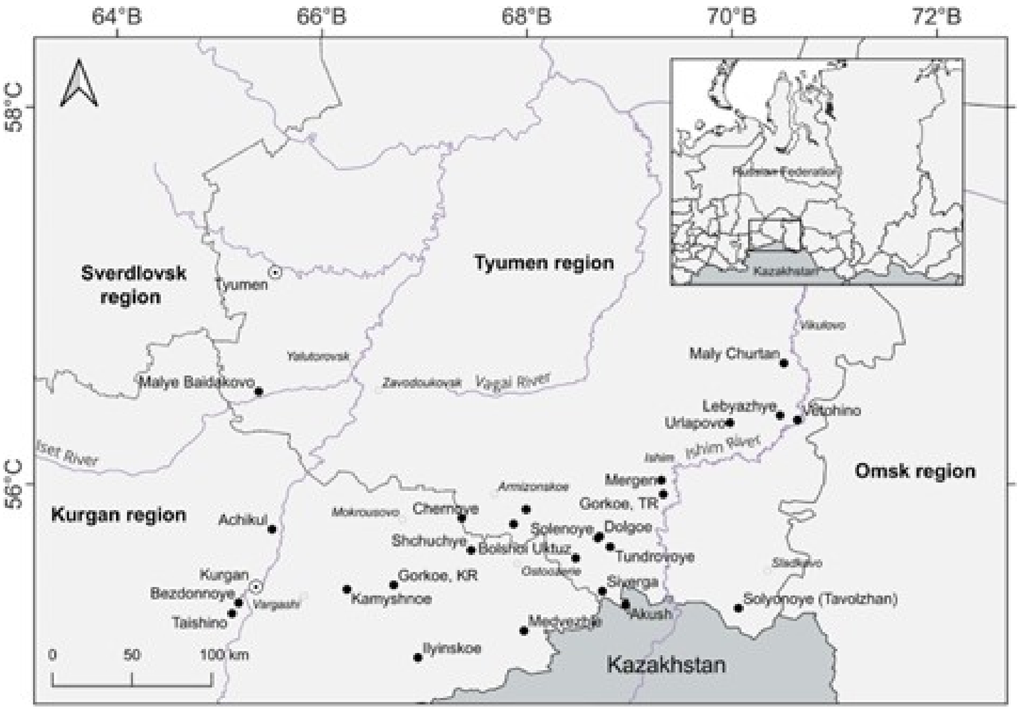

Figure 1. *Location of the studied lakes within the Western Siberian region. Black circle – lakes; black dot in a circle – oblast (region) centers.*

Bird Count Data

The primary method employed was the route census method (Ravkin 1967; Gashev 2014), which utilized an unlimited transect width and calculated bird population density based on mean detection distances. The routes were mapped along the shorelines of the lakes. In addition to the walking routes, bird censuses were con- ducted from a motorboat traveling along the lakes' shores, with regular stops. All birds that took flight and were within the effective detection distance were counted (Gashev 2014).

Lake Characteristics

For each surveyed lake, a comprehensive description was provided, detailing each lake's zone (northern or middle forest–steppe), salinity level (fresh, brackish, saline, brine, and bitter) (Katanayeva and Selyanin 2011; Solodovnikov 2017; List of lakes in the Kurgan region (); List of lakes in the Tyumen region (), area, and the rate of overgrowth (Table 1). In all lakes, current studies on quantitative composition of vegetation have been carried out in all lakes. Three categories of lakes were identified: 1 – lakes poorly overgrown with macrophytes (degree of overgrowth less than 5%); 2 – heavily overgrown lakes are characterized by intensive development of the helophyte zone (degree of overgrowth from 5 to 25%); 3 – eutrophic, strongly overgrown lakes (degree of overgrowth more than 25%) (Lawniczak-Malinska and Achtenberg 2018).

Additionally, Google Earth satellite images were utilized to evaluate the lakes' area. The surveyed lakes are divided by water surface area into the following groups: small (water surface area is less than 1 km²), medium (water surface area is 1.1–50 km²) and large (water surface area is more than 50 km²) (Myakisheva 2009).

Table 1. Lake characteristics

Subzone	Name, administrative location	Salinity	Area, km²	Overgrowth Index*	Research Period
Northern forest–steppe	Lake Mergen, TO, Ishimsky Dist.	fresh	26.20	3	2016
	Lake Vetokhino, TO, Abatsky Dist.	fresh	1.00	2	2015–2016
	Lake Lebyazhye, TO, Abatsky Dist.	fresh	0.41	3	2015–2016
	Lake Urlanovo, TO, Urlanovo Dist.	fresh	3.32	3	2015–2016
	Lake Malyy Churtan, TO, Vikulovsky Dist.	fresh	4.45	2	2015–2016
	Lake Maloye Baydakovo, TO, Isetsky Dist.	fresh	4.31	2	2021
Middle forest–steppe	Lake Achikul, KO, Belozersky Dist.	fresh	12.01	2	2021
	Lake Bezdonnoye, KO, Kurgan	fresh	10.00	3	2012, 2021
	Lake Tayshino, KO, Ketovsky Dist.	brackish	2.70	2	2015, 2021
	Lake Kamyshnoye, KO, Lebyazhevsky Dist.	fresh	1.80	2	2021
	Lake Gorkoye, KO, Lebyazhevsky Dist.	saline	5.00	1	2021
	Lake Medvezhye, KO, Makushinsky Dist.	brine	61.30	1	2021

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Subzone	Name, administrative location	Salinity	Area, km²	Overgrowth Index*	Research Period
	Lake Ilinskoye, KO, Makushinsky Dist.	fresh	0.51	2	2021
	Lake Shchuchye, KO, Mokrousovsky Dist.	saline	40.37	2	2017, 2021
	Lake Solenoye; TO, Berdyuzhsky Dist.	brine	1.09	1	2016–2017,2019,2021–2023
	Lake Dolgoye, TO,	fresh	1.54	2	2019, 2021

	Berdyuzhsky Dist.				
	Lake Chernoye, TO, Armizonsky Dist.	brackish	224.00	3	2016–2017,2021–2022
	Lake Bolshoye Beloye, TO, Armizonsky Dist.	fresh	27.60	3	2016–2017,2021–2022
	Lake Bolshoy Uktuz; TO, Berdyuzhsky Dist.	saline	9.70	2	2016–2017,2019, 2022
	Lake Tavolzhan, TO, Sladkovsky Dist.	saline	98.86	3	2016–2017,2019,2021–2022
	Lake Siverga, TO, Kazansky Dist.	bitter	53.60	1	2016–2017,2019,2021–2022
	Lake Akush (Yakushi); TO, Kazansky Dist.	saline	25.81	2	2002, 2021
	Lake Tundrovo, TO, Berdyuzhsky Dist.	fresh	22.84	3	2016, 2021
	Lake Nyashino, TO, Armizonsky Dist.	fresh	20.70	3	2016, 2021
	Lake Gorkoye, TO,Ishimsky Dist.	bitter	0.74	1	2015–2016

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Note: TO – Tyumen Oblast; KO – Kurgan Oblast; Dist. – District; * lake overgrowth index.

Data analysis

Using data from all censuses, we compiled a bird fauna list for each lake, calculating the number of registered species and their relative abundance (individuals per km²). With this information, we derived bird community diversity indices, including Margalef species richness index (R), Shannon diversity index (H), Simpson’s diversity index (D), Simpson’s dominance index (C), and Pielou’s evenness index (E) (Magurran 2013). Additionally, we calculated the communities’ resistance (UR), resilience (UU), and overall sustainability (U) using diversity indices alongside coefficients of natural subzones and ecosystem succession stages (Gashev 2014; Boldyrev et al. 2021). Our definition of sustainability is the ability of a system to return to its original state after external forces that may alter it cease. Overall sustainability is the sum of resistance and resilience, where resistance refers to a system's ability to withstand external forces, and resilience refers to its ability to return to its original state after those forces cease (Gashev et al. 2015).

The water bodies studied were categorized based on area, salt content, and shore weediness to identify the ecological factors influencing bird community structure, diversity, and sustainability. For each group of lakes, we calculated the mean values of the indices in question and performed pairwise statistical comparisons using the Student T-test. We computed Spearman’s rank correlation coefficient (r) to evaluate correlations between bird community species diversity and sustainability, as well as the properties of the lakes (salinity, area, and aquatic and semi-aquatic vegetation, i.e., weediness) (Gashev et al. 2020). To assess similarities and differences between bird communities in terms of species number, total species density, R, H, D, UR, and UU indices, we employed Euclidean distance, cluster analysis, and a single linkage (nearest neighbor) dendrogram. Statistical data processing was conducted using STATAN 2009, STATISTICA v. 13.0, and Microsoft Excel.

Results

A total of 180 bird species from 12 orders were recorded at the studied water bodies, all typical of the West Siberian forest–steppe wetlands (Ryabitcev 2008, 2014). The most numerous species were Passeriformes (67 species), Charadriiformes (38 species), and Anseriformes (25 species), reflecting the nature of the biotopes.

Lakes in the middle forest–steppe subzone had the highest numbers of bird species and total abundance (individuals/km²). Fresh Lake Nyashino recorded the highest number of bird species (113) and an average total abundance of 728.7 individuals/km². In contrast, bitter Lake Siverga exhibited the highest total abundance of different species (1825.8 individuals/km²) despite having a relatively small number of species (32). The lowest measures were found in the fresh lakes of the northern forest–steppe: Lake Urlanovo (28 species, 55.61 individuals/km²) and Lake Vetokhino (29 species, 87.76 individuals/km²) (Table 1). The mean total bird density was 2.5 times higher in the middle forest–steppe lakes compared to the northern forest– steppe water bodies, a statistically significant difference ($T=9.87$, $DF=25$, $P<0.001$). These findings suggest that the middle forest–steppe lakes have a greater ecological capacity, likely due to the larger heterogeneity of aquatic ecotopes characterized by mosaic growth and high diversity of aquatic plants, as well as the distribution patterns of heat, water, hydrobionts, and semi–aquatic animals. This heterogeneity supports the coexistence of a wider variety of species (nesting, foraging, and moulting, see Ravkin and Bogomolova 2016; Ravkin et al. 2016).

Overall, the bird communities at the studied lakes demonstrate relatively high species diversity indices (Table 2). The highest values of Simpson's index, which emphasizes the most abundant species, were found in the bird communities of middle forest–steppe fresh Lakes Nyashino ($D=6.37$) and Tundrovo ($D=6.12$). The lowest values were recorded in the bird communities of the fresh northern forest–steppe Lakes Mergen ($D=0.97$) and Malyy Churtan ($D=2.08$). The highest values of the Shannon diversity index, which focuses on rare species, were observed in the bird communities of middle forest–steppe fresh Lakes Nyashino ($H=18.35$) and Tundrovo ($H=15.43$), while the lowest values were found in the highly saline middle forest–steppe Lakes Shchuchye ($H=3.38$) and Siverga ($H=3.70$). All examined bird communities exhibited low dominance index values, with the highest, $C=0.20$ (20% of the total), noted for Lake Siverga, where the proportion of its dominant species, the black–headed gull *Chroicocephalus ridibundus* L., 1766, varied from 21% to 83% (Lupinos et al. 2017). Low dominance is particularly characteristic of bird communities during the breeding period, which aligns with the high evenness index values observed across all studied communities, indicating a relatively even distribution of individuals among most species.

Bird communities in most lakes showed Pielou's evenness index values close to 1 (100%). However, two lakes exhibited relatively low evenness indices: in middle forest–steppe bitter Lake Siverga, a single dominant species, the black-headed gull significantly outnumbers others, while northern forest–steppe fresh Lake Malyy Churtan displayed a comparatively low Simpson's diversity index. Comparative analysis of diversity indices indicates that bird communities in middle forest–steppe freshwater lakes exhibit the highest species diversity, high evenness, and low dominance (Table 2). Consequently, we conclude that the species diversity of bird communities is positively correlated with the distribution of subzones and salinity levels.

Table 2. Diversity indices of bird communities in the forest-steppe lakes of Western Siberia

Lake name	S	N	H	D	E	C	UR	UU	U
Northern forest–steppe									
Mergen	58	147.00	8.38	0.97	0.99	0.01	1.54	13.30	14.84
Vetokhino	29	87.76	5.44	4.99	0.93	0.07	1.85	12.07	13.92
Lebyazhye	44	150.51	7.56	5.51	0.96	0.04	1.60	12.90	14.50
Urlanovo	28	55.61	5.76	4.86	0.97	0.03	1.75	10.38	12.13
Malyy Churtan	49	176.02	8.21	2.08	0.85	0.15	1.55	13.02	14.57
Maloye	38	840.03	7.73	5.00	0.96	0.04	1.54	11.17	12.71

Baydakovo									
Middle forest–steppe									
Achikul	57	314.70	10.76	5.50	0.97	0.03	1.36	11.68	13.04
Bezdonnoye	62	401.16	11.34	5.67	0.98	0.02	1.34	11.90	13.24
Tayshino	45	332.19	9.24	5.34	0.97	0.03	1.44	11.62	13.06
Kamyshnoye	60	348.03	10.65	5.55	0.97	0.03	1.37	11.70	13.07
Gorkoye, TO	36	194.07	7.17	4.81	0.96	0.04	1.58	10.69	12.27
Medvezhye	32	172.98	6.49	4.61	0.95	0.05	1.64	10.36	12.00
Ilinskoye	45	1229.16	8.71	5.21	0.97	0.03	1.47	11.37	12.84

Lake name	S	N	H	D	E	C	UR	UU	U
Shchuchye	24	505.55	3.38	3.82	0.90	0.09	2.24	8.12	10.36
Solenoye	23	145.87	5.65	4.37	0.95	0.05	1.76	10.25	12.01
Dolgoye	55	459.98	10.32	5.43	0.97	0.03	1.38	11.61	12.99
Chernoye	36	860.31	4.78	4.72	0.95	0.04	1.94	10.74	12.68
Bolshoye Beloye	31	510.95	4.11	4.24	0.92	0.07	2.04	9.21	11.25
Bolshoy Uktuz	35	1686.75	4.61	4.29	0.90	0.08	1.90	8.92	10.82
Tavolzhan	40	657.71	5.98	4.55	0.93	0.06	1.68	9.56	11.24
Siverga	32	1825.83	3.70	2.92	0.79	0.20	1.85	4.89	6.74
Akush (Yakushi)	33	157.19	7.08	4.76	0.96	0.04	1.59	10.78	12.37
Tundrovo	94	587.48	15.43	6.12	0.98	0.02	1.23	12.20	12.43
Nyashino	113	728.70	18.35	6.37	0.98	0.02	1.18	12.37	13.55
Gorkoye, KO	33	81.63	6.31	4.67	0.97	0.03	1.72	11.78	13.50

Note: S – Number of bird species; N – density (ind./km²); H – Shannon diversity index; D – Simpson's diversity index; C – Simpson's dominance index; E – Pielou's evenness index; UR – resistant sustainability; UU – resilient sustainability; U – overall sustainability.

The analysis of bird population structure in the investigated lakes revealed a group of dominant bird species that account for over 10% of the total bird density. In the northern forest–steppe lakes, this dominant group includes several grass-dwelling species, such as the common reed bunting (*Schoeniclus schoeniclus*, Linnaeus, 1758), which varies in share from 11% at Lake Urlanovo to 23.8% at Lake Maloye Baydakovo. Other species include the sedge warbler (*Acrocephalus schoenobaenus*, Linnaeus, 1758) with a share of 12% at Lake Lebyazhye, and the spotted crake (*Porzana porzana*, Linnaeus, 1766) with a share of 10% at Lake Maloye Baydakovo (see Suppl. material 1: Table 1S).

In the middle forest–steppe lakes of Kurgan Oblast, the dominant group also includes bush-dwelling species like the common reed bunting, sedge warbler, and corn crake (*Crex crex*, Linnaeus, 1758). At the middle forest–steppe water bodies of Tyumen Oblast, the dominant species shift to include aquatic and semi-aquatic birds, such as the common pochard (*Aythya ferina*, Linnaeus, 1758), Eurasian coot (*Fulica atra*, Linnaeus, 1758), and black-headed gull (see Suppl. material 1: Table 1S).

For instance, during the four-year research period at Lake Bolshoy Uktuz, the common pochard was the dominant species, although its proportion of total bird abundance decreased over time: 41% (86.6 individuals/km²) in 2016, 25% (24.5 individuals/km²) in 2017, 13% (25.3 individuals/km²) in 2019, and only 11.1% (29.5 individuals/km²) by 2022. This decline is attributed to the comfort provided by the weeds lining the lake's shores, which are significant for the waterfowl biotope structure, offering spaces for foraging, resting, and molting of diving ducks. These birds find safety not in dense reed stands but in expansive, deep stretches of water.

In nearly all fresh and slightly saline lakes, the Eurasian coot is dominant, with its share varying from 12% at Lake Bolshoye Beloye to 20% at Lake Chernoye (see Suppl. material 1: Table 1S). The Eurasian coot demonstrates wide ecological plasticity, adapting its habitat choices to different life cycle stages and feeding on a variety of readily available plant forage. It is also strongly territorial, defending its nest and chicks from intruders, and has few natural enemies, making it less of a target for hunters compared to other duck species.

Compared to the northern forest–steppe water bodies, the middle forest–steppe lakes show a slightly higher abundance and dominance of small waders. The little stint (*Calidris minuta*, Pallas, 1776) is more common at lakes Akush (10.2%), Tavolzhan (11%), and Chernoye (15%), while the red-necked phalarope (*Phalaropus lobatus*, Linnaeus, 1758) is more abundant at lakes Chernoye (13%), Bolshoye Beloye (16%), and Siverga (19%). These species are the most numerous transient waders found in the middle forest–steppe salt lakes.

The black-headed gull is one of the most numerous gulls in the Western Siberian forest–steppe zone. It is moderately selective in nesting site choice, often nesting in colonies across various lake types. The dominance of the black-headed gull in the middle forest–steppe lakes is linked to the presence of numerous transient bird flocks; for example, in 2017, it accounted for 83% of total bird abundance at Lake Siverga.

Discussion

Empirical data collected from various animal groups indicate that sustainability indices serve as more informative and sensitive indicators of community health compared to diversity indices. This is because sustainability indices consider not only diversity but also natural zone characteristics and the stage of ecosystem succession (Gashev et al. 2015). High species diversity indices correlate with elevated levels of resilience and overall sustainability in the studied bird communities (Table 2). This relationship may be attributed to the optimal zone pattern in the forest-steppe region, which provides favorable conditions of heat, moisture, and biological resources. Additionally, the water bodies examined are situated within a Ramsar site, where specific species and aquatic ecosystems are protected (Ravkin et al. 2016; Gashev and Kurhinen 2015).

A comparative analysis of sustainability indices reveals that in different bird communities, the values for U, UR, and UU are closely aligned, with overall sustainability primarily influenced by the resilient component (Table 3). This observation suggests that the ecosystems under investigation are relatively undisturbed, supporting our conclusion regarding the positive impact of bird species diversity conservation measures in the water bodies of southern Western Siberia. The highest values of UU and U are found in the bird communities of the northern forest- steppe fresh lakes Mergen, Malyy Churtan, and Lebyazhye. Despite their varying sizes, these water bodies share a common feature: a high level of overgrowth with macrophytes (2–3 points).

In contrast, the highest UR values are recorded in middle forest-steppe bird communities, specifically at saline Lake Shchuchye (UR=2.24) and fresh Lake Bolshoye Beloye (UR=2.04). Although these two water bodies differ in several characteristics, including salinity, area, and weediness, both are influenced by human economic activities. Near Lake Bolshoye Beloye, there are arable lands yielding high grain crops, while Lake Shchuchye supports a commercial fishery that attracts frequent human visitation.

A bird community characterized by the lowest values of UU and U is found in the Siverga lake, which is a large middle forest-steppe lake. This community is notable for its high salinity and the absence of aquatic plants. In contrast, the bird communities of Lakes Nyashino and Tundrovo exhibit comparatively low UR values alongside high U and UU values (refer to Table 3). This suggests that these water bodies have undergone the least transformation in their biological communities, likely due to their location within specially protected natural areas that implement conservation measures and limit economic activities.

Table 3. Statistical comparison of avian communities across different lakes, highlighting diversity, abundance, and species richness

Lake types	Species number (S)	Total density (N)	Resistant sustainability (UR)	Resilient sustainability (UU)	Overall sustainability (U)
Fresh (n=14)	54.50±6.42	431.22±88.61	1.51±0.1**	11.78±0.3	13.29
Saline (n=11)	33.54±1.89**	601.83±187.17	1.76±0.1	9.79±0.60**	11.55
Large lakes (n=14)	50.57±6.92	529.40±116.51	1.61±0.08	10.54±0.55	12.15
Small lakes (n=11)	38.54±2.99	476.86±164.44	1.63±0.05	11.37±0.36	13.00
Overgrown (n=10)	56.22±9.82	455.49±95.08	1.58±0.10	11.39±0.49	12.97
Moderately overgrown (n=10)	42.73±3.59	557.94±150.71	1.61±0.08	11.09±0.42	12.70
Not overgrown (n=5)	31.20±2.18	484.08±335.97	1.71±0.05	9.59±1.21	11.30
Northern forest–steppe (n=6)	41.00	242.82	1.64	12.14	13.78
Middle forest–steppe (n=19)	46.63	589.49	1.62	10.51	12.13

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Note: S – number of bird species; N – density (individuals/km^2); UR – resistant sustainability; UU – resilient sustainability; U – overall sustainability; n – sample size; ** – significant difference at $p<0.01$.

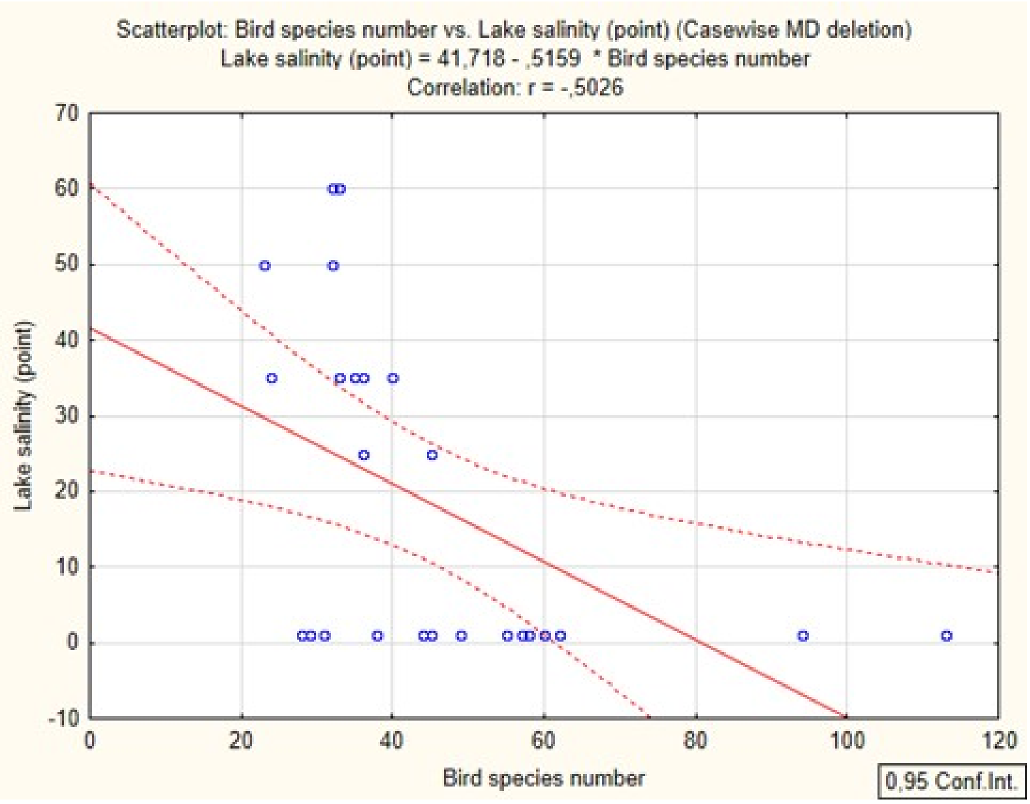

Figure 2. *Relationship between bird species diversity and lake salinity (confidence intervals indicated by dashed lines).*

A pairwise intergroup comparison of bird communities from various lake types revealed significant differences between those in fresh and saline water bodies regarding the mean number of bird species, as well as their resistant and resilient sustainability values. On average, the number of bird species recorded in salt lakes is significantly lower than in fresh water bodies (T=3.79, DF=17, P<0.01). Additionally, bird communities in saline lakes show significantly higher mean values of resistant sustainability (T=2.63, DF=23, P<0.01) but lower mean values of resilient sustainability (T=3.25, DF=23, P<0.01), resulting in overall lower sustainability values (see Table 3).

There is a significant inverse correlation (r =-0.50, T=3.47, DF=25, P<0.01) between the number of species recorded at the lakes and the water salinity level, indicating that as salinity levels increase, the number of bird species tends to decrease. This trend suggests that high salt concentrations in the lakes hinder the growth of macrophytes and hydrobionts, which in turn reduces the lakes' protective and foraging capacities.

There are notable correlations between lake salinity and various indices of aquatic bird communities. Specifically, significant relationships were found with Simpson’s diversity index (r=-0.41, T=2.18, DF=25, P<0.05), Simpson’s dominance index (r=0.40, T=2.10, DF=25, P<0.05), resilient sustainability (r=-0.62, T=3.78, DF=25, P<0.01), and resistant sustainability (r=0.43, T=2.32, DF=25, P<0.01).

Conversely, no reliable correlation exists between bird density and the overgrowth of banks with aquatic and coastal vegetation (r=0.19; P>0.05), nor between lake area and the examined bird community parameters (r=0.11; P>0.05).

The statistical analysis included a comparison of bird communities in northern and middle forest-steppes, revealing no significant differences. In terms of species count, no significant differences were observed (T=1.59, DF=23, P>0.05). This lack of variation may be attributed to a recent northward shift of southern species, moving from the middle to the northern forest-steppe, likely due to global warming and increased continentality in the local climate. This phenomenon has led to a flattening of previous gradients in a meridional direction (Gashev and Kurhinen 2015; Ravkin et al. 2016; Gashev et al. 2017).

Cluster analysis of resistant and resilient sustainability indicates that the aquatic bird communities in the northern and middle forest-steppe do not form distinct partitions based on subzone; instead, they create mixed clusters (Fig. 3). This pattern holds true for bird communities across lakes, irrespective of their size, vegetation, or salinity. The significant influence of these factors on bird communities, with each factor exhibiting either synergistic or antagonistic effects in specific instances, complicates clear differentiation during analysis.

Nonetheless, it is possible to identify two complex geographical clusters, which we can label as ‘eastern’ and ‘western’ (Fig. 3A). The eastern cluster primarily consists of lakes from the Pritobolny District forest-steppe (Kurgan Oblast), excluding lakes Mergen and Lebyazhye, and is characterized by high overall sustainability and comparatively higher UU/UR ratios. In contrast, the western cluster comprises lakes from the Vagay–Ishim forest-steppe (Tyumen Oblast), which exhibit low overall sustainability. These two clusters are separated by a third cluster of six lakes (Vetokhino, Urlanovo, Medvezhye, Solenoye, Shchuchye, and Malyy Churtan) that demonstrate high overall sustainability but low UU/UR values. Although these six lakes are part of a macrocluster with the western cluster (Fig. 3B), their geographical positioning aligns them more closely with the eastern cluster.

This clustering effectively groups highly saline lakes, highlighting the similarities between the most saline lakes, Medvezhye and Solenoye. The western cluster lacks subdivisions, while the eastern cluster features Siverga saline lake, which is distinct due to its large area, minimal overgrowth, and the lowest UU/UR ratio. Additionally, there is a separate cluster comprising two fresh, overgrown lakes – Tundrovo and Nyashino – that exhibit the highest UU/UR ratio values. Analyzing smaller lake clusters is less meaningful without first categorizing them based on their ecological and geographical characteristics.

A crucial aspect of bird conservation is the protection of unique specially desig- nated areas within the study sites across Kurgan and Tyumen Oblasts (Lupinos and Pokazaneva 2017; Lupinos and Pokazaneva 2018; Ivanova et al. 2021). Among the 25 lakes studied, thirteen are situated within protected areas. Our findings indicate that, when controlling for other factors, the number of bird species in protected areas is 1.7 times greater than in unprotected areas ($T=2.34$, $DF=12$, $P<0.05$).

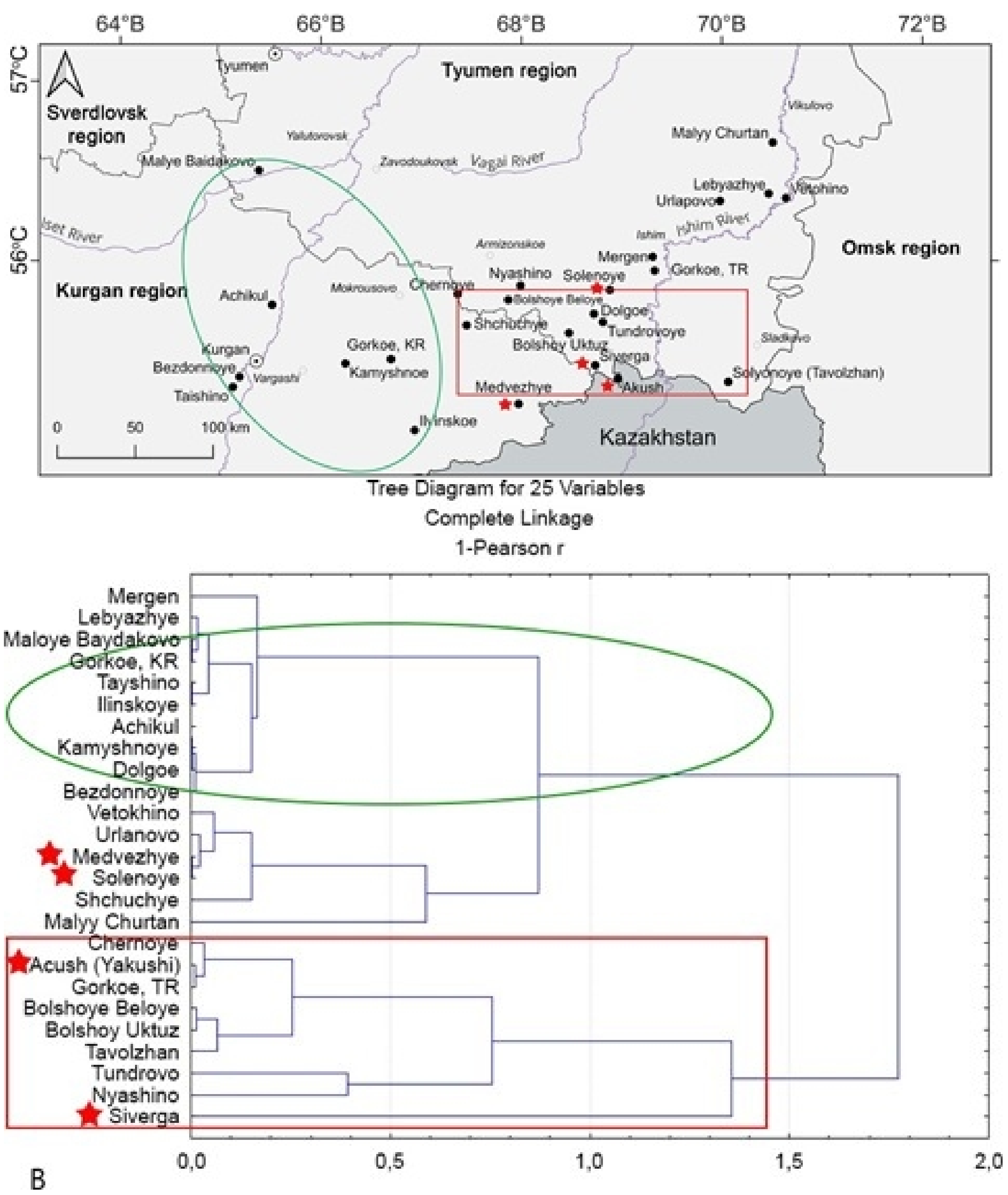

Figure 3. *Distribution of bird communities in the studied lakes, categorized by their resistant and resilient sustainability values:* ***A*** *– spatial representation of the primary clusters; black circle – lakes; black dot in a circle – oblast (region) centers;* ***B*** *– dendrogram illustrating the relationships among the clusters; green – western cluster (Pritobolny District forest–steppe); red – eastern cluster (Vagay–Ishim forest–steppe); red stars – highly saline lakes.*

During our research, we identified 23 bird species requiring conservation and rehabilitation measures, which are listed in the regional Red Data Books (Lupinos et al. 2016; Lupinos et al. 2017; Lupinos and Pokazaneva 2017; The Red Data Book of Tyumen Oblast 2020; The Red Data Book of Kurgan Oblast 2012), the Red Data Book of the Russian Federation (2021), and the IUCN Red List (2016). This includes two critically endangered species, Great white pelican *Pelecanus onocrotalus* Linnaeus, 1758 and White-headed duck *Oxyura leucocephala* (Scopoli, 1769), which are recognized in both the National Red Book and the IUCN Red List. Throughout the study period, the highest number of rare species was recorded at the middle forest–steppe fresh lakes Tavolzhan (11 species), Nyashino (10 species), and Tundrovo (9 species). These lakes are renowned for their high density of migrating aquatic, semi–aquatic, and carnivorous birds, and they hold the status of state reserves and important bird areas (Lupinos and Pokazaneva 2018; Ivanova et al. 2021).

Conclusions

At 25 lakes in Tyumen and Kurgan Oblasts, 180 aquatic and semi-aquatic bird species were observed, representing two-thirds of the 270 species registered in the region's wetlands. The bird communities reflect the habitat structure, with 35% from Charadriiformes and Anseriformes, and 37.2% from Passeriformes. Dominant species are influenced more by lake ecotopes than geographical subzones, as evidenced by similarities in species across northern and middle forest–steppe lakes. A total of 23 bird species from the Red Data Books were recorded, including two critically endangered species, highlighting the importance of these water bodies for bird conservation at multiple levels.

The lakes exhibit high species diversity, evenness, and resilience, with significant differences between subzones; middle forest–steppe lakes have 2.5 times greater bird abundance and higher species counts than northern lakes. This suggests greater ecological capacity in middle forest–steppe water bodies due to increased habitat heterogeneity. Middle forest–steppe lakes show the highest species diversity and low dominance, while northern lakes, overgrown with macrophytes, support resilient communities. Lake Siverga, however, has the lowest resilience and diversity, indicating that salinity impacts community structure. Saline lakes have fewer species but higher resistant sustainability, with species numbers inversely correlated to salinity. No significant relationship exists between lake area and bird community characteristics, as diversity peaks along shorelines. Cluster analysis reveals that total bird abundance is the primary factor in grouping lakes. Despite varying salinity and overgrowth, Shchuchye and Bolshoye Beloye lakes support resilient bird communities due to anthropogenic influences.

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Supplementary material 1

Table 1S. Dominant and rare bird species at the investigated lakes

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