

Article

Factors Affecting the Winter Distribution of Birds in Forests at the Eastern Edge of Europe

Arthur Askeyev ¹, Oleg Askeyev ¹, Igor Askeyev ¹ and Tim Sparks ^{2,3,*}

¹ Biomonitoring Laboratory, Institute of Problems in Ecology and Mineral Wealth, Tatarstan Academy of Sciences, Dauruskaya Str., 28, Kazan 420087, Russia; art.regulus@mail.ru (A.A.); parus.cyanus@rambler.ru (O.A.); archaeozoologist@yandex.ru (I.A.)

² Department of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71c, 60-625 Poznan, Poland

³ Museum of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

* Correspondence: thspark@btopenworld.com

Simple Summary: The climate of the study area, deep within the Eurasian land mass, varies greatly from warm summers to harsh winter conditions. Here we investigate birds in forests before and after the winter solstice for five years starting in winter 2018/9. Their distribution and abundance changed with respect to geographical location, forest composition, and food supply. Abundance was lower later in winter. However, even in this remote location, climate change is having an impact, with a greater diversity of bird species under more recent milder winters. Further change is expected under anticipated future warming.

Abstract: We show for the first time the results of a study into the spatial distribution of birds in forests at the eastern edge of Europe (Republic of Tatarstan, Russia) and changes from early to late winter. A transect method was used to census randomly selected plots spread over a large geographical area in the winters 2018/9–2022/3. We used regression and ordination methods to assess the influence of key environmental factors on species richness, total density of birds, biological diversity, and the probabilities of occurrence of individual species. The most abundant bird species in early winter was the Willow Tit, and in the late winter was the Common Redpoll. Compared with the end of the 20th century, the number of wintering bird species has increased in the study area, likely due to climate warming. Species richness, total density, and the Shannon Index of diversity were higher in early winter than in late winter. Species richness and the Shannon Index were also higher at low elevations and in the west of the study region. Our research shows strong ecological-geographical differences in the preferences of individual bird species in the studied forests. However, almost without exception, birds had a higher probability of occurrence at lower elevation and toward the west.

Keywords: Tatarstan; spatial distribution; occurrence; latitude; longitude



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1. Introduction

Winter is a critical period for most living organisms [1] living in temperate and boreal latitudes and directly affects the dynamics of bird populations in these latitudes [2]. Winter is a unique period that allows us to study the spatial distribution of not only individual species, but also the whole bird population. However, the spatial distribution of birds in winter remains poorly studied [3]. In Europe, such research is quite rare and is mainly confined to urban areas and usually without division into specific biotopes [4–12]. In the era of rapid climate change [3,13–18] forest ecosystems are fragile and the rational use and protection of biological diversity in them is only possible given a knowledge of the characteristics of the animal communities occupying them [19]. Climate change greatly affects the distribution and density of birds [20], as well as influencing the functioning of forest ecosystems [21,22]. In this regard, forests and the living organisms inhabiting them need accurate monitoring in a long-term context. In addition to gaining knowledge

on the spatial distribution of bird species, such monitoring can also contribute to autecological research [23–27]. In particular, by assessing the degree of spatial contiguity of different species, it is possible to more objectively and in more detail identify interspecies relationships and thereby supplement the understanding of the structure of communities.

The spatial heterogeneity of the bird population can be influenced by changes in natural and climatic conditions, both during the breeding and wintering periods. Winter conditions vary more geographically than summer conditions [28–30]; therefore, it is critical to understand how species distribute spatially in response to winter conditions, not just during the warmer seasons of the year.

As we have previously shown on the basis of many years of research, the main abiotic factors of the biological impact of winter conditions on birds are temperature, snow cover, and food resources [3,16,31], which are often closely interrelated. However, the interaction between the use of habitat by birds and spatial changes in natural and climatic conditions during winter in Eastern Europe is still poorly studied.

In this study, we attempted to understand how habitat influences the spatial heterogeneity of species during winter in Eastern Europe. Using data from the monitoring of wintering birds over 5 years, covering 83 species in the Republic of Tatarstan (eastern part of European Russia), we tried to answer the following questions: (1) Are there differences in the total density and species richness of the bird population between early and late winter? (2) Is there a spatial difference in bird assemblages and in individual bird species? (3) Which, if any, environmental variables affect these differences?

2. Materials and Methods

2.1. Study Area

The Tatarstan Republic is located at the eastern edge of the European continent (Figure 1) between 53°58' N and 56°40' N, 47°15' E and 54°15' E. The overall human population density is ca. 60/km², but less than a quarter live in rural areas. The region has an extensive mosaic of forest landscapes (22% by area) with a transition of forest tree species from north to south, which is of considerable interest when studying the distribution of forest bird species [32]. The southern or southwestern limits of Siberian Spruce (*Picea obovata*), European Spruce (*Picea abies*), and Siberian Fir (*Abies sibirica*) occur within Tatarstan. In addition, Tatarstan is close to the northern limit of Pedunculate Oak (*Quercus robur*). The forests are heterogeneous and the study area is large (67,838 km², 460 km west to east, 290 km north to south) [33]. The relief of the study area is very varied, ranging from 53 to 380 m above sea level [33]. The length of daylight in the capital city of Kazan varies from 7 h on the shortest day (December 20–24) to 11 h on March 5, the longest day in our study period. The climate in winter is harsh in a European context. The minimum temperature, so far, in the 21st century was −38.8 °C [3], and the number of days per year with temperatures below −25 °C can reach 20 days [16]. Snow cover starts in November and can lie for more than 150 days per winter, while the depth of snow cover in some years can exceed 1 m [31]. Some more details on the study winters are given in Appendix A. Despite the extreme severity of the region within Europe, the climate in Tatarstan continues to warm significantly, leading to changes in bird abundance and distribution, and the occurrence of bird species new to the region [16]. All these factors make Tatarstan an interesting region for studying the spatial distribution of its bird population and can serve as an example for further work on zoogeography in Europe.

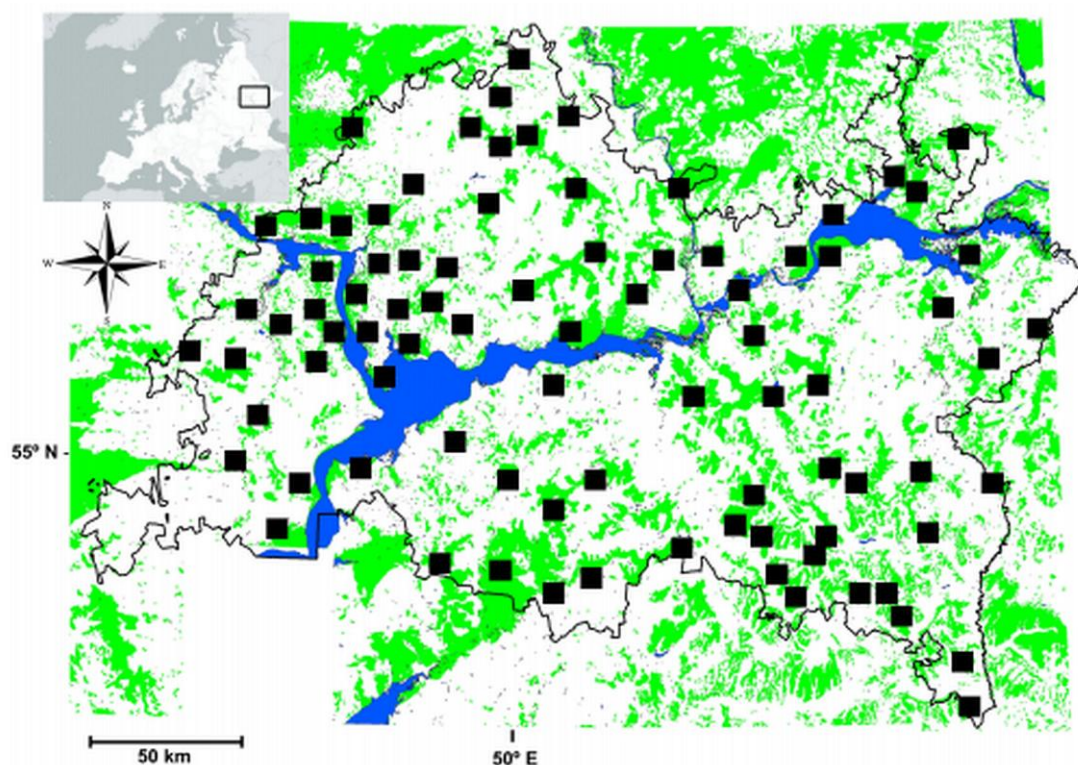


Figure 1. Distribution of sampling sites (black squares) in Tatarstan (inset shows location within Europe). Green shading indicates forests.

2.2. Bird Data

Birds were recorded in winter (1 November–5 March) for five years November 2018–March 2023. Throughout the study periods, average temperatures were invariably sub-zero and to our knowledge, no summer migrant bird species were present. We divided winter into two periods centered around the winter solstice, and for simplicity refer to these as early winter (day length decreasing, 1 November–25 December) and late winter (day length increasing, 26 December–5 March). Fieldwork was carried out in the morning according to Y.S. Ravkin’s transect methods [34] without a fixed strip width with subsequent conversion to the area using group mean detection ranges. This approach considers birds recorded by sight and by call within the forest in three distance bands, estimated by eye, from the transect (0–25 m, >25–100 m, >100–300 m) and estimates densities in numbers per km², using a conversion formula; i.e., the sum of $40 \times$ the near count, $10 \times$ the middle count, and $3 \times$ the far count, all divided by the transect length (in km) [3]. In the current work, we calculated summaries and species densities in each year and used the average over the five years in subsequent analysis. Average data were used to smooth out annual fluctuations in the number of birds and annual differences of an ecological or phenological nature [35]. Only three observers (AO, OA, IA) carried out the surveys on foot or by skiing. Bird names were taken from Gill et al. [36]. In early winter, 63 sites were recorded (Figure 1), with a total area of more than 1200 km². In late winter 58 sites were recorded with a total area of 1100 km². Each site consisted entirely of a forest and riparian woodland transect of 6–20 km and each was visited 2–4 times each year in both early winter and in late winter. The total length of the transect routes was more than 7000 km. In 80% of the sites, the bird census was conducted every year with equal intensity. For each site, separately for early and late winter, we calculated the mean number of species of birds, hereafter species richness, the total density of birds, the Shannon index of diversity (H'), and the density and frequency of occurrence (in %) of each individual species of birds. We recorded the following five explanatory variables: elevation above sea level (m), latitude ($^{\circ}$ N), longitude ($^{\circ}$ E), conifer

cover (%), and the abundance of Rowan (*Sorbus aucuparia*) berries (visual observations on the Kapper scale [37], a 6-point ordinal scale from “none” to “very good”, see [31]).

2.3. Data Analysis

2.3.1. Relationship between Species Richness, Total Density, and Shannon Index with Environmental Variables

During analysis, the predictor variables were assessed for multicollinearity using Variance Inflation Factor (VIF) and Tolerance, which revealed low values of both, so all five predictors were retained. The nature and strength of relationships between the dependent variables and the five environmental predictor variables were examined using generalized linear models with a normal error structure, separately for early and late winter. Selection of the best-fit model was based on the lowest Akaike Information Criterion (AIC) values. We used paired *t*-tests to compare the dependent variables between early and late winter. Differences between the two winter periods in each dependent variable were tested for, and passed, normality using Shapiro–Wilk tests.

2.3.2. Relationship between Bird Species and Environmental Variables

For ordination and individual species models, we included only those bird species that were found in more than six forest sites. Thus, the data matrix consisted of five environmental variables and 55 bird species in early winter and five environmental variables and 45 bird species in late winter. Redundancy Analysis (RDA) was used to examine the environmental variables that determined the occurrence of bird species assemblages in forests. Ordination was carried out on presence-absence data. The nature and strength of relationships between the occurrence of individual bird species and environmental variables were examined using generalized linear models with a binomial error structure. In order to estimate the accuracy of the models, we used the area under the ROC curve (AUC), which indicates the predictive performance as an index ranging from 0.5 to 1, where the accuracy of the model is considered as follows: 0.90–1.00 excellent; 0.80–0.90 good; 0.70–0.80 fair; 0.60–0.70 poor; and 0.50–0.60 fail [38]. Calculation and visualization were carried out in PAST version 4.14 and MINITAB 19. No adjustment was made to *p*-values for multiple tests and the reader should be aware that, with a large number of tests, some significant results may arise by chance.

3. Results

3.1. General Information on Bird Species

In total, 83 bird species were recorded in the forests of Tatarstan during the winter period (Table 1).

Table 1. List of the 83 bird species recorded, their scientific and common names, and codes as used in later figures along with their frequency of occurrence (in %, *n* = 63 for early winter; *n* = 58 for late winter) and density (individuals/km² ± SE) in Tatarstan in early and late winter (before and after the winter solstice).

No.	Species Name and Code	Early Winter		Late Winter	
		Occurrence %	Density /km ²	Occurrence %	Density /km ²
1	<i>Ardea cinerea</i> —Grey Heron	0	0	1.7	0.01 ± 0.01
2	<i>Accipiter gentilis</i> —Eurasian Goshawk (Acge)	25.4	0.21 ± 0.07	25.9	0.16 ± 0.06
3	<i>Accipiter nisus</i> —Eurasian Sparrowhawk (Acni)	22.2	0.12 ± 0.03	10.3	0.08 ± 0.04
4	<i>Buteo lagopus</i> —Rough-legged Buzzard (Bula)	44.4	0.88 ± 0.19	13.8	0.08 ± 0.04
5	<i>Aquila chrysaetos</i> —Golden Eagle	6.3	0.02 ± 0.01	5.2	0.01 ± 0.01
6	<i>Aquila heliaca</i> —Eastern Imperial Eagle	3.2	0.02 ± 0.01	0	0
7	<i>Haliaeetus albicilla</i> —White-tailed Eagle (Haal)	31.8	0.28 ± 0.08	37.9	0.31 ± 0.11

Table 1. Cont.

No.	Species Name and Code	Early Winter		Late Winter	
		Occurrence %	Density /km ²	Occurrence %	Density /km ²
8	<i>Falco columbarius</i> —Merlin	7.9	0.09 ± 0.05	3.4	0.01 ± 0.01
9	<i>Falco peregrinus</i> —Peregrine Falcon	6.3	0.02 ± 0.01	3.4	0.01 ± 0.01
10	<i>Lyrurus tetrrix</i> —Black Grouse (Lyte)	38.1	0.46 ± 0.13	18.9	0.27 ± 0.12
11	<i>Tetrao urogallus</i> —Western Capercaillie	6.3	0.05 ± 0.03	3.4	0.06 ± 0.05
12	<i>Tetrastes bonasia</i> —Hazel Grouse (Tebo)	25.4	0.86 ± 0.30	12.1	0.45 ± 0.25
13	<i>Perdix perdix</i> —Grey Partridge (Pepe)	20.6	1.15 ± 0.48	24.1	5.21 ± 2.27
14	<i>Scolopax rusticola</i> —Eurasian Woodcock	7.9	0.13 ± 0.07	0	0
15	<i>Larus cachinnans</i> —Caspian Gull	3.3	0.21 ± 0.19	1.7	0.01 ± 0.01
16	<i>Columba oenas</i> —Stock Dove (Cooe)	15.9	0.08 ± 0.03	6.9	0.07 ± 0.05
17	<i>Columba palumbus</i> —Common Wood Pigeon	3.2	0.04 ± 0.03	0	0
18	<i>Bubo bubo</i> —Eurasian Eagle-Owl	1.6	0.01 ± 0.01	0	0
19	<i>Asio otus</i> —Long-eared Owl	1.6	0.01 ± 0.01	1.7	0.14 ± 0.14
20	<i>Aegolius funereus</i> —Boreal Owl (Aefu)	9.5	0.04 ± 0.02	10.3	0.05 ± 0.03
21	<i>Glaucidium passerinum</i> —Eurasian Pygmy Owl (Glpa)	15.9	0.10 ± 0.04	10.3	0.08 ± 0.04
22	<i>Athene noctua</i> —Little Owl	3.2	0.01 ± 0.01	1.7	0.01 ± 0.01
23	<i>Surnia ulula</i> —Northern Hawk-owl	4.8	0.06 ± 0.04	0	0
24	<i>Strix aluco</i> —Tawny Owl	4.8	0.03 ± 0.02	0	0
25	<i>Strix uralensis</i> —Ural Owl	34.9	0.29 ± 0.09	25.9	0.22 ± 0.08
26	<i>Dendrocopos leucotos</i> —White-backed Woodpecker (Dele)	61.9	2.26 ± 0.41	63.8	1.68 ± 0.29
27	<i>Dendrocopos major</i> —Great Spotted Woodpecker (Dema)	84.1	16.20 ± 1.89	81.0	13.12 ± 1.59
28	<i>Dendrocopetes medius</i> —Middle Spotted Woodpecker (Deme)	9.5	0.14 ± 0.09	8.6	0.15 ± 0.11
29	<i>Dryocopus martius</i> —Black Woodpecker (Drma)	60.3	1.16 ± 0.19	65.5	1.81 ± 0.38
30	<i>Dryobates minor</i> —Lesser Spotted Woodpecker (Drmi)	60.3	1.86 ± 0.41	44.8	1.01 ± 0.18
31	<i>Picoides tridactylus</i> —Eurasian Three-toed Woodpecker (Pitr)	25.4	1.11 ± 0.32	18.9	0.47 ± 0.21
32	<i>Picus canus</i> —Grey-headed Woodpecker (Pica)	23.8	0.35 ± 0.17	37.9	0.35 ± 0.08
33	<i>Picus viridis</i> —Green Woodpecker (Pivi)	15.9	0.12 ± 0.04	12.1	0.06 ± 0.02
34	<i>Eremophila alpestris</i> —Horned Lark	7.9	0.22 ± 0.13	5.2	0.02 ± 0.01
35	<i>Motacilla alba</i> —White Wagtail	3.2	0.03 ± 0.02	0	0
36	<i>Lanius excubitor</i> —Great Grey Shrike	20.6	0.20 ± 0.09	8.6	0.33 ± 0.18
37	<i>Corvus cornix</i> —Hooded Crow (Coco)	68.3	2.32 ± 0.62	81.0	3.35 ± 0.89
38	<i>Corvus corax</i> —Common Raven (Cocr)	92.1	3.91 ± 0.45	84.4	2.59 ± 0.34
39	<i>Corvus monedula</i> —Jackdaw (Como)	36.5	0.91 ± 0.41	37.9	0.61 ± 0.21
40	<i>Garrulus glandarius</i> —European Jay (Gagl)	79.4	4.87 ± 0.68	67.2	2.89 ± 0.49
41	<i>Nucifraga caryocatactes</i> —Eurasian (Spotted) Nutcracker (Nuca)	33.3	0.66 ± 0.22	18.9	0.29 ± 0.11
42	<i>Perisoreus infaustus</i> —Siberian Jay	4.8	0.15 ± 0.10	0	0
43	<i>Pica pica</i> —Eurasian Magpie (Pipi)	61.9	4.13 ± 0.87	68.9	6.38 ± 1.19

Table 1. Cont.

No.	Species Name and Code	Early Winter		Late Winter	
		Occurrence %	Density /km ²	Occurrence %	Density /km ²
44	<i>Prunella montanella</i> —Siberian Accentor	7.9	0.21 ± 0.13	0	0
45	<i>Prunella modularis</i> —Dunnock	6.3	0.16 ± 0.12	0	0
46	<i>Bombycilla garullus</i> —Waxwing (Boga)	57.1	12.48 ± 2.48	51.7	16.68 ± 4.01
47	<i>Regulus regulus</i> —Goldcrest (Rere)	66.7	41.01 ± 6.21	53.4	14.73 ± 2.63
48	<i>Phylloscopus collybita</i> —Common Chiffchaff	3.2	0.03 ± 0.02	0	0
49	<i>Erithacus rubecula</i> —European Robin (Erru)	33.3	1.20 ± 0.35	3.4	0.05 ± 0.04
50	<i>Phoenicurus ochruros</i> —Black Redstart	7.9	0.17 ± 0.08	1.7	0.02 ± 0.02
51	<i>Turdus merula</i> —Common Blackbird (Tume)	9.5	0.29 ± 0.14	1.7	0.02 ± 0.02
52	<i>Turdus philomelos</i> —Song Thrush (Tuph)	15.9	0.78 ± 0.36	1.7	0.01 ± 0.01
53	<i>Turdus pilaris</i> —Fieldfare (Tupi)	55.6	7.21 ± 2.13	34.0	6.02 ± 1.93
54	<i>Turdus viscivorus</i> —Mistle Thrush (Tuvi)	15.9	0.56 ± 0.21	5.1	0.08 ± 0.05
55	<i>Turdus iliacus</i> —Redwing (Tuil)	22.2	0.79 ± 0.35	1.7	0.03 ± 0.03
56	<i>Aegithalos caudatus</i> —Long-tailed Tit (Aeca)	92.1	56.60 ± 5.84	70.7	27.71 ± 3.92
57	<i>Cyanistes caeruleus</i> —Blue Tit (Cyca)	84.1	31.31 ± 3.60	79.3	17.42 ± 4.38
58	<i>Cyanistes cyaneus</i> —Azure Tit (Cycy)	9.5	0.24 ± 0.14	10.3	0.31 ± 0.16
59	<i>Lophophanes cristatus</i> —Crested Tit (Locr)	9.5	2.46 ± 1.14	13.8	3.19 ± 1.29
60	<i>Parus major</i> —Great Tit (Pama)	87.3	28.81 ± 4.39	74.1	21.31 ± 6.07
61	<i>Periparus ater</i> —Coal Tit (Peat)	65.1	52.30 ± 8.27	56.9	16.81 ± 2.73
62	<i>Poecile montanus</i> —Willow Tit (Pomo)	88.9	61.80 ± 7.20	84.4	33.91 ± 4.41
63	<i>Poecile palustris</i> —Marsh Tit (Popa)	57.1	17.29 ± 3.19	62.1	11.32 ± 1.94
64	<i>Sitta europaea</i> —Eurasian Nuthatch (Sieu)	92.1	34.42 ± 3.21	81.0	15.00 ± 2.63
65	<i>Certhia familiaris</i> —Eurasian Treecreeper (Cefa)	85.7	23.91 ± 3.02	75.9	8.91 ± 1.25
66	<i>Passer montanus</i> —Eurasian Tree Sparrow (Pamo)	19.1	1.15 ± 0.44	20.7	2.04 ± 0.79
67	<i>Troglodytes troglodytes</i> —Eurasian Wren (Trtr)	19.1	0.61 ± 0.25	1.7	0.02 ± 0.02
68	<i>Acanthis flammea</i> —Common Redpoll (Acfl)	80.9	36.22 ± 5.39	77.6	37.71 ± 7.16
69	<i>Carduelis carduelis</i> —European Goldfinch (Caca)	61.9	9.80 ± 1.99	48.3	13.73 ± 3.51
70	<i>Chloris chloris</i> —European Greenfinch (Chch)	33.3	0.96 ± 0.32	32.8	1.79 ± 0.68
71	<i>Spinus spinus</i> —Eurasian Siskin (Spsp)	66.7	19.12 ± 3.05	48.3	10.54 ± 2.30
72	<i>Carpodacus sibiricus</i> —Siberian Long-tailed Rosefinch	7.9	0.17 ± 0.10	6.9	0.19 ± 0.13
73	<i>Pinicola enucleator</i> —Pine Grosbeak (Pien)	19.1	0.44 ± 0.23	5.2	0.05 ± 0.03
74	<i>Loxia curvirostra</i> —Red Crossbill (Locu)	52.4	14.70 ± 4.14	48.3	11.02 ± 3.67
75	<i>Loxia leucoptera</i> —Two-barred Crossbill (Lole)	14.3	0.98 ± 0.38	6.9	0.21 ± 0.15
76	<i>Loxia pytyopsittacus</i> —Parrot Crossbill	0	0	1.7	0.01 ± 0.01
77	<i>Pyrrhula pyrrhula</i> —Common Bullfinch (Pypy)	92.1	27.70 ± 3.01	89.7	15.51 ± 2.89
78	<i>Coccothraustes coccothraustes</i> —Hawfinch	7.9	0.05 ± 0.02	8.6	0.39 ± 0.27
79	<i>Fringilla montifringilla</i> —Brambling	7.9	2.76 ± 1.38	1.7	0.05 ± 0.05
80	<i>Fringilla coelebs</i> —Eurasian Chaffinch	7.9	1.83 ± 1.31	5.2	0.07 ± 0.04
81	<i>Linaria cannabina</i> —Common Linnet (Lica)	22.2	0.64 ± 0.25	18.9	1.75 ± 1.23
82	<i>Emberiza citrinella</i> —Yellowhammer (Emci)	46.0	4.17 ± 1.36	12.1	0.66 ± 0.36
83	<i>Emberiza rustica</i> —Rustic Bunting	7.9	0.26 ± 0.12	1.7	0.02 ± 0.02

3.2. Early Winter

In early winter, 81 bird species were recorded (Table 1). Species richness in this period varied from 6 to 58 species per plot (mean \pm SE 26.8 ± 1.4). The total density of birds varied from 49.6 to 1327.0 individuals per km² (mean \pm SE 541.3 ± 32.4). The Shannon index ranged from 1.36 to 2.96 (mean \pm SE 2.43 ± 0.05).

The 10 most widespread birds in early winter were: Common Bullfinch, Long-tailed Tit, Common Raven, Eurasian Nuthatch, Willow Tit, Great Tit, Eurasian Treecreeper, Blue Tit, Great Spotted Woodpecker, and European Jay. These species were recorded in more than 75% of sites (Table 1). The most numerous species of birds (i.e., by abundance) were: Willow Tit, Long-tailed Tit, Coal Tit, Goldcrest, Common Redpoll, Eurasian Nuthatch, Blue Tit, Great Tit, Common Bullfinch, Eurasian Treecreeper, Siskin, Marsh Tit, Great Spotted Woodpecker, Red Crossbill, and Waxwing. The average density of these bird species in the study area exceeded 10/km² (Table 1). Together, these 15 species accounted for 87% of all birds recorded.

3.3. Late Winter

In late winter, 72 bird species were recorded (Table 1). Compared to early winter, the following 11 species were not observed: Eastern Imperial Eagle, Eurasian Woodcock, Common Wood Pigeon, Eurasian Eagle-owl, Northern Hawk-owl, Tawny Owl, White Wagtail, Siberian Jay, Siberian Accentor, Dunnock, and Common Chiffchaff. In contrast, Grey Heron and Parrot Crossbill were only recorded in late winter. Species richness varied from 6 to 42 species per plot (mean \pm SE 21.1 ± 1.1). Species richness was significantly higher in early winter than in late winter ($t = 6.29$, $p < 0.001$). The total density of birds varied from 59.4 to 660.6 individuals/km² (mean \pm SE 333.7 ± 20.6). The total density was significantly higher in early winter than in late winter ($t = 6.51$, $p < 0.001$). The following nine bird species were recorded in more than 75% of the plots: Common Bullfinch, Willow Tit, Common Raven, Hooded Crow, Eurasian Nuthatch, Great Spotted Woodpecker, Blue Tit, Common Redpoll and Eurasian Treecreeper. The most numerous species of birds were Common Redpoll, Willow Tit, Long-tailed Tit, Great Tit, Waxwing, Eurasian Nuthatch, Blue Tit, Coal Tit, Common Bullfinch, Goldcrest, Great Spotted Woodpecker, European Goldfinch, Marsh Tit, Red Crossbill, and Eurasian Siskin. The average density of these species of birds exceeded 10/km² (Table 1). Together, these 15 species accounted for 83% of all birds recorded. The Shannon index ranged from 1.33 to 2.91 (mean \pm SE 2.24 ± 0.06). The value of the Shannon index in late winter was significantly less than in early winter ($t = 3.23$, $p = 0.002$).

3.4. Relationships of Species Richness, Total Density, and Shannon Index with Environmental Variables

3.4.1. Early Winter

Models with the lowest AIC are shown in Table 2a. Models for species richness and total bird density included four variables. Both models included longitude, conifer cover, and Rowan berries. Species richness (Figure 2A) and total bird density were higher toward the west, in higher conifer cover, and on sites with higher yields of Rowan. Species richness was also higher on low-elevation sites and total bird density was higher toward the north. The model for the Shannon index included two variables and was higher at lower elevation sites (Figure 3A) and toward the west.

Table 2. Coefficients and model summary of the relationship between species richness, total density, and Shannon index, with environmental variables in Tatarstan in (a) early winter and (b) late winter. Environmental variables included in the models are abbreviated as follows: elevation above sea level (Elev), latitude (Lat), longitude (Long), conifer cover (Con), Rowan berries (Row). Selected models are based on lowest AIC.

	Constant	Elev	Lat	Long	Con	Row	AIC
(a) Early winter							
Species richness	1.9	−0.4		−3.3	0.7	1.6	479.7
Total bird density	8.5		2.1	−3.2	4.1	2.6	849.3
Shannon index (H')	3.2	−0.2		−0.9			214.4
(b) Late winter							
Species richness	1.1	−0.6		−1.6			414.9
Total bird density	7.6			−3.0		5.2	753.9
Shannon index (H')	3.1	−0.2		−0.3	0.3		211.2

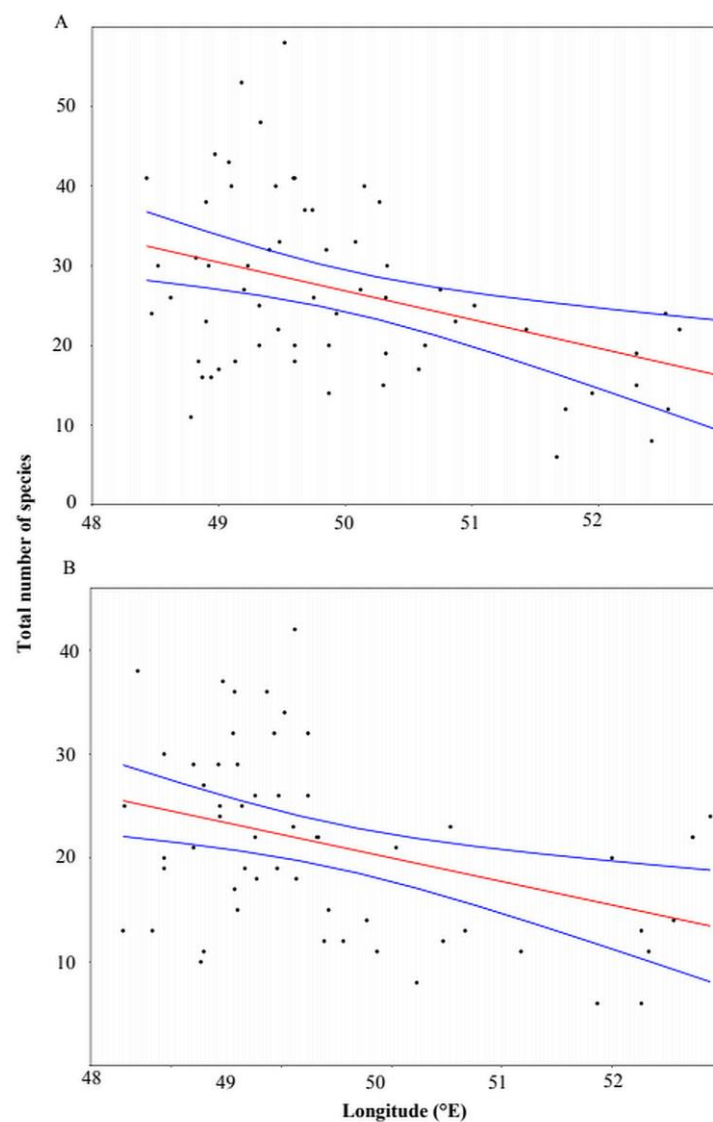


Figure 2. Relationship (red line) between species richness (total number of species) and longitude in Tatarstan (A) in early winter, (B) in late winter. Blue lines represent the 95% confidence interval.

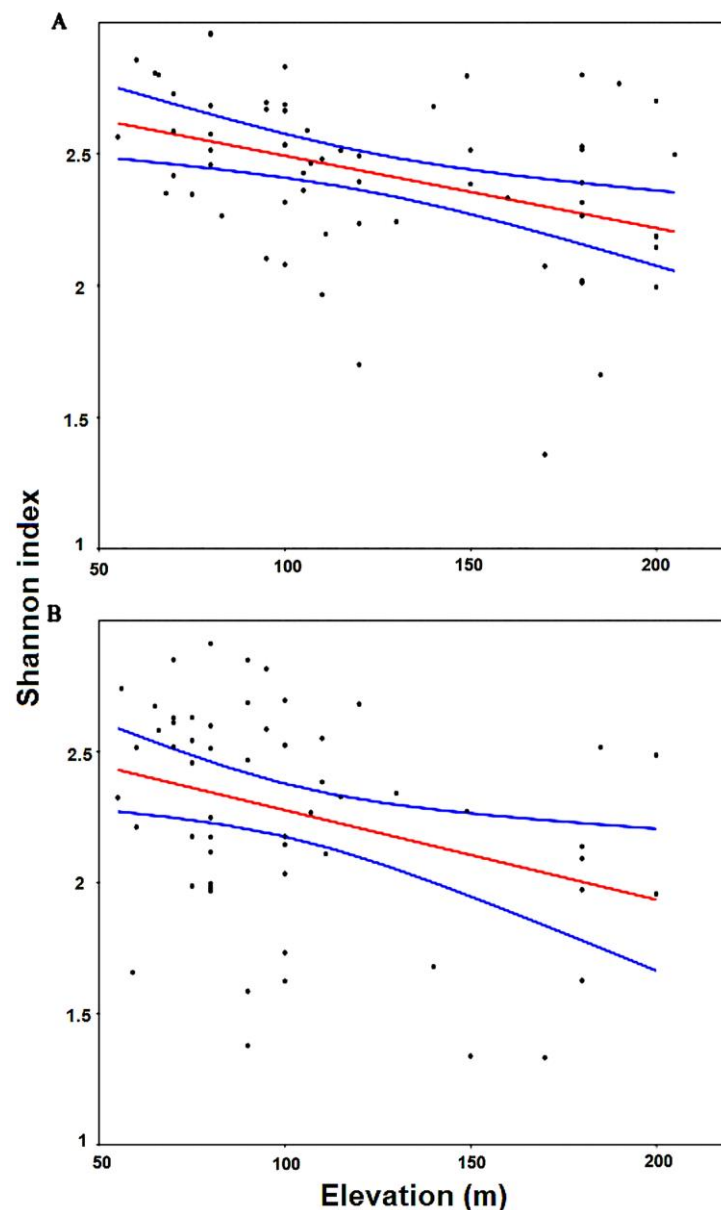


Figure 3. Relationship (red line) between Shannon index and elevation in Tatarstan (**A**) in early winter, (**B**) in late winter. Blue lines represent the 95% confidence interval.

3.4.2. Late Winter

Models with the lowest AIC are shown in Table 2b. Models for species richness and the Shannon index included two and three predictor variables, respectively. Both models included elevation and longitude, with higher values toward the west (Figure 2B) and at low elevations (Figure 3B). The Shannon index was also higher under greater conifer cover. The model for total bird densities included two variables; densities were higher toward the west (Figure 3B) and with greater amounts of Rowan berries.

3.5. Relationship between Bird Assemblages and Environmental Variables

3.5.1. Early Winter

The first two axes of the RDA explained 79.8% of the total variance in bird population in early winter (Figure 4). The first axis of ordination explained 53.9% of the variance and was mainly associated ($p < 0.001$) with conifer cover and latitude. In general, the first axis showed a change in the bird population from the north-boreal group of birds (left-hand side) to a group of birds that prefer deciduous forests in the south (right-hand side) in

winter. At the species level, these results confirmed the fact that “boreal” species, such as Red Crossbill, Two-barred Crossbill, Pine Grosbeak, Three-toed Woodpecker, Boreal Owl, Goldcrest, Coal Tit, Willow Tit, Hazel Grouse, Eurasian Nutcracker, European Robin, and Great Spotted Woodpecker were associated with coniferous forests and the northern regions of our study area. In contrast, the White-backed Woodpecker, Goldfinch, Blue Tit, Yellowhammer, Jackdaw, Grey Partridge, Middle Spotted Woodpecker, Hooded Crow, Common Linnet, Stock Dove, and Eurasian Tree Sparrow were associated with deciduous trees and the south.

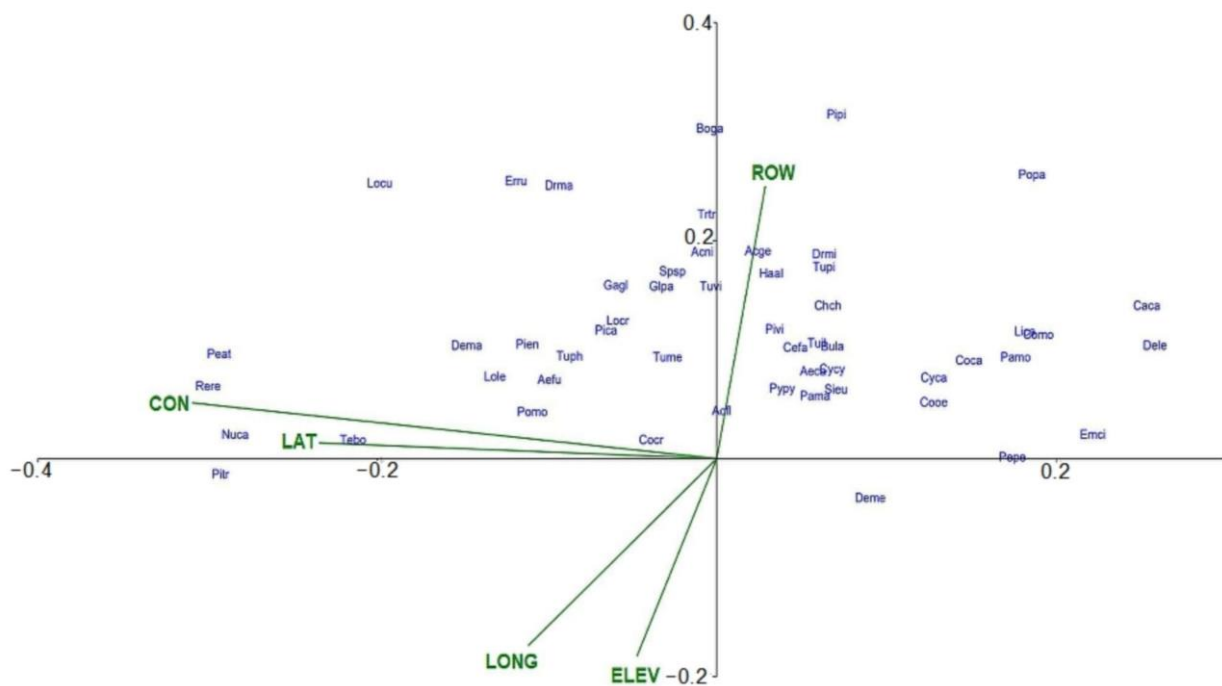


Figure 4. Biplots of first versus second axes of Redundancy Analysis (RDA), showing the relative influence of each environmental variable on the distribution of bird species in Tatarstan in early winter. Environmental variables shown as green vectors, species (for abbreviations e.g., Pipi = *Pica pica* Eurasian Magpie, see Table 1) shown as blue labels.

The second axis explained 25.8% of the variance and was strongly associated with longitude, elevation, and Rowan berries. No individual bird species were identified that preferred eastern, high altitude, low berry yield sites.

3.5.2. Late Winter

The first two axes of the RDA explained 82.8% of the total variance in bird populations in late winter (Figure 5). The first axis accounted for 64.3% of the variance and, as in early winter, was mainly associated ($p < 0.05$) with conifer cover and latitude. As for early winter, there was a strong gradient between north-boreal birds and those that preferred deciduous forests.

The second axis explained 18.5% of the variance and was associated with elevation and, to a lesser extent, longitude and Rowan berries. There was a stronger influence of elevation on the species composition of birds than in early winter, but again there were no birds that preferred higher elevations.

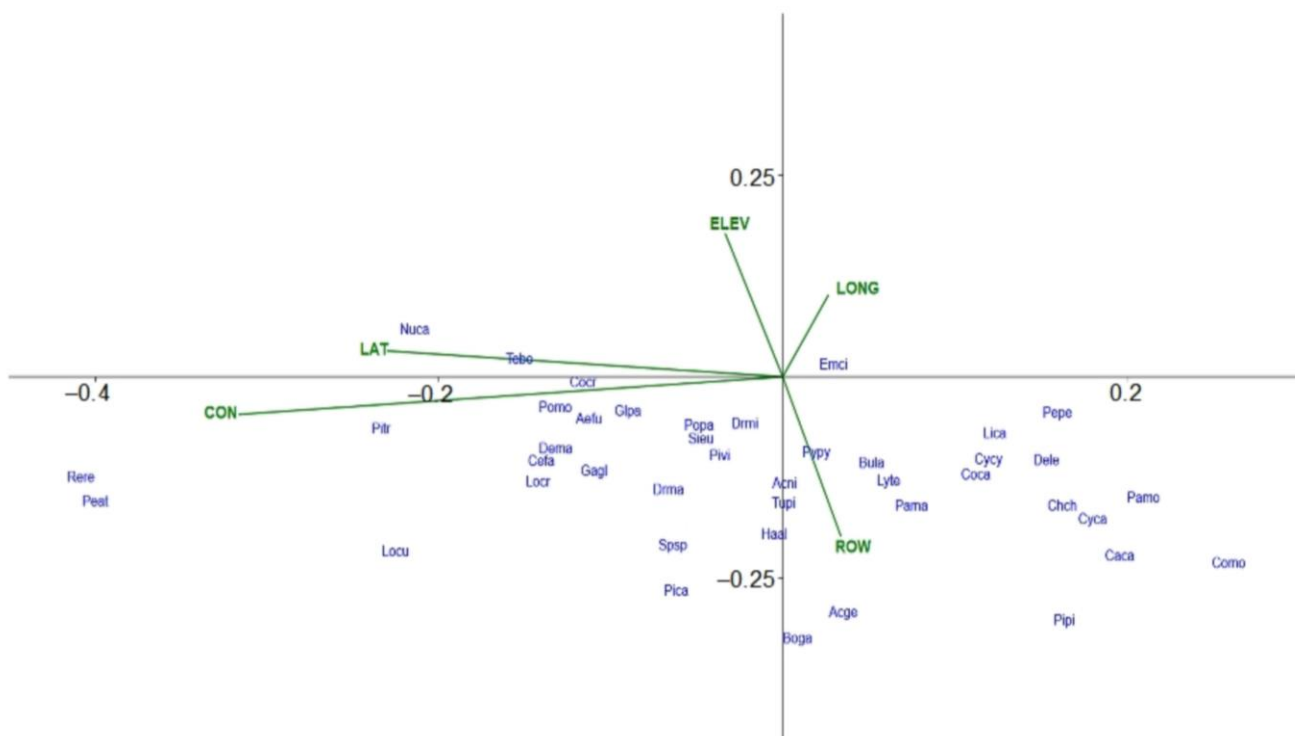


Figure 5. Biplot of first versus second axes of Redundancy Analysis (RDA), showing the relative influence of each environmental variable on the distribution of bird species in Tatarstan in late winter. Environmental variables shown as green vectors, species (for abbreviations e.g., Pipi = *Pica pica* Eurasian Magpie, see Table 1) shown as blue labels.

3.6. Factors Explaining the Occurrence of Bird Species

3.6.1. Early Winter

Significant models ($p < 0.05$) were achieved for 53 out of 55 bird species. Models had satisfactory predictive power (AUC) varying from 0.701 to 0.983 and nine models were classed as excellent (Table 3). Thirty bird species were strongly associated with conifer cover, and 19 with latitude (12 positive and seven negative). In general, species can be divided into groups. For example, the probability of occurrences for the Boreal Owl, Three-toed Woodpecker, Eurasian Nutcracker, and Crested Tit at latitudes south of 55°N was close to or equal to zero, for Hazel Grouse and Pine Grosbeak it did not exceed 7%, for Coal Tit 15%, and for Goldcrest and Common Crossbill less than 25% (Figure 6). Common Raven and Great Spotted Woodpecker were more evenly distributed but preferred the north; at latitudes north of 56°N the probability of their occurrence was above 90%. In contrast, the probability of occurrence for Goldfinch, Blue Tit, Hooded Crow, and White-backed Woodpecker at latitudes south of 55°N was above 90%. Grey Partridge and Azure Tit also preferred the south; the probability of occurrence for the Grey Partridge north of 56°N did not exceed 20%, and Azure Tit under 10%. For Jackdaw, there was a systematic decrease in the probability of occurrence from south to north. Nineteen species were also associated with longitude, with all cases preferring the west. Elevation is featured in 12 models, with all preferring lower elevations. All 10 species significantly associated with Rowan berries had a positive relationship.

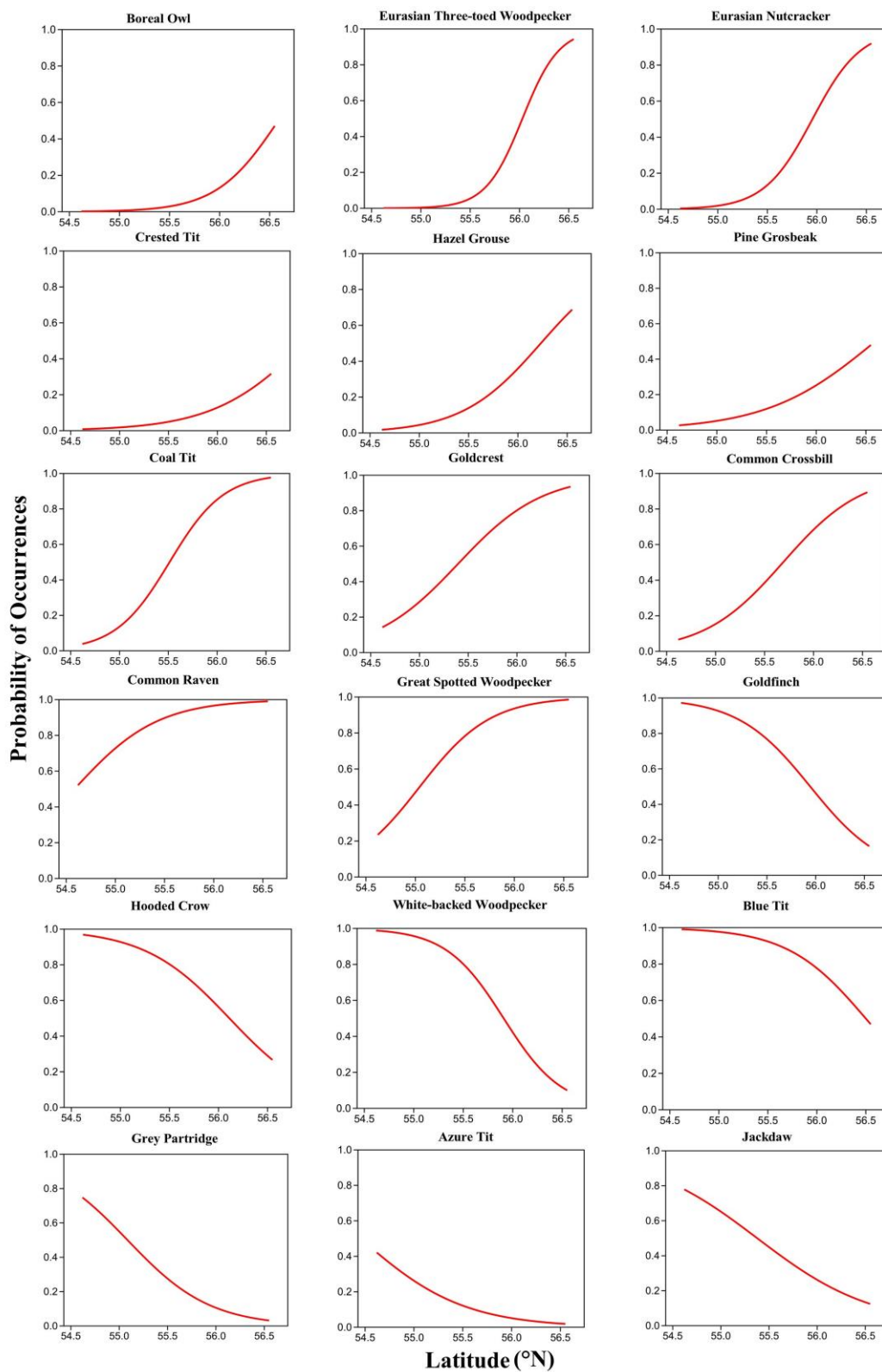


Figure 6. A selection of bird species showing contrasting patterns between the probability of occurrence and latitude in Tatarstan in early winter.

Table 3. Coefficients and model summary for the relationship between presence/absence of 55 bird species and environmental variables in Tatarstan in early winter. Environmental variables included in models are abbreviated as follows: elevation above sea level (Elev), latitude (Lat), longitude (Long), conifer cover (Con), Rowan berries (Row).

Species Name	Constant	Elev	Lat	Long	Con	Row	AIC	AUC
Goshawk	1.4	−0.3		−1.1	0.6		60.1	0.818
Sparrowhawk	3.1			−0.7	0.4		67.2	0.795
Rough-legged Buzzard	3.5			−0.8			72.4	0.701
White-tailed Eagle	1.1	−0.2					71.4	0.704
Black Grouse							No model	
Hazel Grouse	−2.9		2.4		0.4		59.9	0.831
Grey Partridge	2.2		−2.9		−0.4		56.1	0.831
Stock Dove	−0.6				−0.4		51.9	0.715
Boreal Owl	1.7		3.2	−1.5	0.5		33.5	0.924
Eurasian Pygmy Owl	4.1			−1.1	0.2		48.6	0.851
Ural Owl							No model	
White-backed Woodpecker	2.5		−3.3		−1.3		59.9	0.870
Great Spotted Woodpecker	−0.7		3.3		0.2		36.7	0.911
Middle Spotted Woodpecker	−0.9				−0.1		35.9	0.797
Black Woodpecker	2.9	−0.9		−0.6	0.3		70.5	0.756
Lesser Spotted Woodpecker	3.4			−0.7			81.0	0.702
Three-toed Woodpecker	2.0		3.4		0.5		46.5	0.923
Grey-headed Woodpecker	1.5	−0.4			0.2		58.3	0.830
Green Woodpecker	4.6			−1.6			51.2	0.726
Hooded Crow	1.5		−3.1			1.3	68.5	0.800
Common Raven	−1.3		2.4				36.0	0.724
Jackdaw	−2.6	−0.2	−0.4		−0.4	0.8	71.7	0.841
European Jay	3.4			−0.7	0.3		62.4	0.711
Eurasian Nutcracker	−1.4		2.5		0.3		61.7	0.848
Eurasian Magpie	3.4	−0.4					59.0	0.892
Waxwing	−1.5					2.1	62.2	0.858
Goldcrest	−4.4		3.5		0.2		42.7	0.946
European Robin	2.6			−0.6	0.3		74.7	0.727
Song Thrush	−1.8					0.8	51.8	0.798
Fieldfare	−0.7					0.9	80.7	0.701
Mistle Thrush	−2.8					0.9	54.0	0.796
Redwing	2.9					0.7	68.5	0.724
Common Blackbird	−1.9					1.3	39.9	0.842
Long-tailed Tit	3.3			−0.6			40.2	0.728
Blue Tit	1.4		−2.5				53.4	0.728
Azure Tit	2.0	−0.2	−3.5				25.6	0.962
Crested Tit	3.3		5.8	−5.4	0.7		21.3	0.983
Great Tit	2.2	−0.2					63.9	0.733

Table 3. Cont.

Species Name	Constant	Elev	Lat	Long	Con	Row	AIC	AUC
Coal Tit	−1.6		3.8		0.4		51.4	0.901
Willow Tit	−0.2				0.2		36.6	0.903
Marsh Tit	4.0	−0.2		−1.3			57.7	0.891
Eurasian Nuthatch	3.7			−0.7			35.1	0.824
Eurasian Treecreeper	3.4			−0.6			50.7	0.741
Eurasian Tree Sparrow	−0.8	−0.2			−0.7		50.6	0.846
Eurasian Wren	4.6	−0.2		−1.5			55.1	0.820
Common Redpoll	−1.4				−0.2		61.1	0.704
Goldfinch	3.6		−0.8	−0.7	−0.3		71.6	0.811
Greenfinch	2.4			−0.5			80.9	0.701
Siskin	−4.2		1.3	−0.5	0.3		79.5	0.706
Pine Grosbeak	3.9		2.1		0.3	0.6	56.7	0.822
Red Crossbill	4.9		3.4		0.6		68.2	0.836
Two-barred Crossbill	4.8				0.7		38.4	0.910
Common Bullfinch	1.1					1.0	55.4	0.766
Common Linnet	1.5	−0.1			−0.5		60.2	0.795
Yellowhammer	0.9				−0.3		79.4	0.731

3.6.2. Late Winter

Significant models ($p < 0.05$) were achieved for 43 of 45 bird species. Models had satisfactory predictive power (AUC); varying from 0.629 to 0.973 and eight models were classed as excellent (Table 4). Twenty-six bird species were strongly associated with conifer cover, 14 with elevation (all associated with lower elevation), and 13 with latitude (six positive and seven negative). Twelve species were associated with longitude; in all but one case toward western sites. Five species were positively associated with Rowan berries.

Table 4. Coefficients and model summary for the relationship between presence/absence of 45 bird species and environmental variables in Tatarstan in late winter. Environmental variables included in models are abbreviated as follows: elevation above sea level (Elev), latitude (Lat), longitude (Long), conifer cover (Con), Rowan berries (Row).

Species Name	Constant	Elev	Lat	Long	Con	Row	AIC	AUC
Goshawk	2.2	−0.4					62.0	0.784
Sparrowhawk	3.2			−2.9	0.4		36.9	0.821
Rough-legged Buzzard	0.7	−0.3					47.3	0.670
White-tailed Eagle	2.0	−0.4					73.0	0.702
Black Grouse	1.4	−0.3					55.1	0.701
Hazel Grouse	−5.9		4.5		0.5		28.1	0.933
Grey Partridge	2.3		−4.1				57.1	0.767
Boreal Owl	2.3		4.1		0.4		34.7	0.933
Eurasian pygmy Owl	5.8			−1.3	0.3		37.1	0.824
Ural Owl							No model	

Table 4. Cont.

Species Name	Constant	Elev	Lat	Long	Con	Row	AIC	AUC
White-backed Woodpecker	2.6				−0.3		75.7	0.701
Great Spotted Woodpecker	2.6				0.4		52.5	0.777
Black Woodpecker	2.2				0.1		69.3	0.657
Lesser Spotted Woodpecker	1.3	−0.1					78.9	0.634
Three-toed Woodpecker	3.1		5.4		0.7		37.1	0.915
Grey-headed Woodpecker	3.5	−0.2		−0.7			39.9	0.787
Green Woodpecker	5.8			−1.2			43.4	0.691
Hooded Crow	1.6		−2.9			0.8	56.2	0.770
Common Raven	0.5		2.3		0.3		45.5	0.789
Jackdaw	1.6	−0.1	−2.9		−0.2	0.9	64.4	0.852
European Jay	−1.0				0.2		73.4	0.661
Eurasian Nutcracker	−2.1		3.4	0.3	0.5		38.4	0.927
Eurasian Magpie	3.6	−0.3			−0.2		65.6	0.782
Waxwing	0.7	−0.1				1.2	67.7	0.812
Goldcrest	−4.0				1.0		39.5	0.949
Fieldfare	−2.2					0.9	78.7	0.782
Long-tailed Tit							No model	
Blue Tit	2.1		−3.1	−0.7	−0.2		54.2	0.841
Azure Tit	3.7	−0.8			−0.4		30.0	0.920
Crested Tit	3.2			−4.2	0.4		21.0	0.973
Great Tit	2.4	−0.1					67.7	0.654
Coal Tit	−2.7				1.9		40.4	0.938
Willow Tit	0.5				0.6		45.5	0.785
Marsh Tit	−3.6			−1.1			60.3	0.719
Eurasian Nuthatch	2.9			−0.6			57.8	0.760
Eurasian Treecreeper	0.3				0.3		62.9	0.706
Eurasian Tree Sparrow	1.5	−0.2	−2.6		−0.3		52.0	0.821
Common Redpoll	2.5			−0.5			62.9	0.654
Goldfinch	1.8		−2.8	−0.5			79.5	0.721
Greenfinch	1.5	−0.1			0.2		72.8	0.700
Siskin	1.5		2.7		0.3		78.0	0.714
Red Crossbill	−1.2				0.3		64.1	0.779
Common Bullfinch	3.2	−0.1	−5.7			0.4	37.7	0.846
Common Linnet	5.1			−1.1	−0.3		54.8	0.758
Yellowhammer	−2.5				−0.6		69.9	0.629

4. Discussion

Our study is the first to analyze the spatial distribution of birds in forests in the extreme east of the European continent in winter. The total density of birds significantly decreased in late winter compared to early winter; mainly due to a decrease in the number of Common Bullfinch and small insectivorous birds: Goldcrest, Coal Tit, Willow Tit, Long-tailed Tit, Blue Tit, Eurasian Treecreeper, and Eurasian Nuthatch. The main reason for the decrease in

the abundance of these bird species is likely harsh winter conditions leading to mortality [3]. Furthermore, the probability of occurrence and density for all bird species including true thrushes, Rough-legged Buzzard, Eurasian Wren, European Robin, and Yellowhammer were also significantly reduced. For example, the European Robin, which was recorded in more than a third of the sites in early winter, was found in only two sites in late winter. In Poland, such a pattern was not apparent, species richness and total abundance were higher in late winter than in early winter [10]. We believe these differences were associated with the milder climate in Poland compared to our study area in the far east of Europe. But even under the harsh climate of our study area, there have been marked changes in the species composition of birds in winter due to a rapidly warming climate. Reduced extreme weather [31] and warming in winter [16] allow some bird species to remain in the study area throughout the winter. For example, at the end of the 20th century [32], European Robin and Song Thrush did not occur in Tatarstan in late winter. Bird diversity in Tatarstan forests, as indicated by the Shannon index, in early winter is slightly higher than in late winter. This is due to the larger number of bird species in early winter and a reduced dominance of common species.

As in our study, the total abundance of birds in Poland was higher toward the west [10]. None of the bird species in our study preferred eastern sites, with the exception of the Eurasian Nutcracker in late winter. This general pattern was to be expected because, in both Tatarstan and Poland, the climate is milder in winter toward the west. None of our studied bird species in winter had a higher probability of occurrence at higher elevations. Higher elevations are also associated with harsher environments and therefore do not attract birds in winter. It is interesting that the response of the bird community to elevation was similar to that of fish communities in the same region [39]. In winter, during very harsh conditions and low temperatures, when the birds need additional food resources [31,40,41], total bird density was higher in areas with more Rowan berries. The positive effect of Rowan berries on bird diversity was also noted in Finland [42,43]. As well as specialized species of frugivores, other birds, for example, from the corvid family, also actively eat Rowan berries in winter. But the main factor influencing the distribution of bird species, both in the early and late winter, was conifer cover. Bird species richness was higher in mixed forests with a predominance of conifers. These habitats are most attractive for different bird species since they offer more protection from severe weather, and greater productivity in the winter season [40].

Comparing our results on individual bird species with those from elsewhere in Europe generates marked differences. In Poland, the most common bird species in winter were the Great Tit, Blue Tit, Eurasian Magpie, and Common Blackbird [10]. The latter two species are rarely found in winter in Tatarstan. Furthermore, the probability of occurrence of Hawfinch and Common Chaffinch was much higher in Poland than in our study. Other species in Poland, such as Common Buzzard and Syrian Woodpecker, are not yet found in Tatarstan in the winter in forests. In contrast, the probability of occurrence of Rough-legged Buzzard, White-tailed Eagle, Common Redpoll, Pygmy Owl, Common Raven, Eurasian Treecreeper, Willow Tit, Long-tailed Tit, Lesser Spotted Woodpecker, and Black Woodpecker is much higher in our region. In Poland, these species are rarer and are recorded in no more than 10% of sites [10]. These differences are due to the historical development of these regions, and to climatic conditions affecting bird assemblages both directly and indirectly. Despite marked differences in the bird assemblages in different parts of Europe, some bird species have similar ecological and geographical preferences. For example, the preference of Three-toed Woodpecker for coniferous trees in Europe has been reported [44,45] and confirmed in our study. In Finland, as in our study, the Goldfinch, Yellowhammer, and Blue Tit preferred deciduous forests in the south [5]. Our reported preference for the Boreal Owl for conifer forests was also noted in Finland [46]. A strong association between Waxwing and Rowan yield has been noted in Finland [47,48].

Our research on the spatial distribution of individual species of birds shows strong spatial differentiation. In early winter, we found contrasting preferences between individual

bird species, which can be broadly divided into two groups: the first group preferred northern latitudes and forests with a predominance of conifer species, and the second group was represented by species that live mainly in deciduous forests in the south. For Great Spotted and White-backed Woodpeckers, we observe contrasting latitudinal distributions within Tatarstan. For Coal Tit and Blue Tit, we also found similar differences in spatial distribution. These species are evolutionarily close and, perhaps, we see here not just different geographical preferences, but a spatial replacement of one species with the other. In late winter, we saw a similar pattern but the number of species preferring southern regions and deciduous forests was higher. In late winter, we recorded a more even pattern of bird species on a latitudinal gradient and a stronger relationship with elevation. In our opinion, this is due to the much more severe climatic conditions in late winter. Some bird species appeared indifferent to environmental variables, for example, the Ural Owl. Long-tailed Tit, a common bird species in our study, shows a high degree of indifference to forest types and the geographical location of the forest area. This species is not tied to specific biotopes and has an extremely high degree of mobility [3].

In the era of socialization of science, when a huge number of volunteers are involved in the study of the spatial distribution of birds, it is necessary to properly organize the long-term monitoring of bird population dynamics. Birds can easily move around forests but prefer the environmental conditions to which they are most evolutionarily adapted [24,40]. Our studies in Tatarstan show that both the probability of occurrence of individual species and the total density of birds are heterogeneous. For example, if we had conducted most of our surveys south of 55°N, the probability of occurrence of Coal Tits would have been less than 15%, and their density at most sites would have been zero. In some published research, there is an indication that the abundance of boreal bird species has decreased significantly [49–51]. But a large number of those studies were conducted in southern regions [52]. Our study shows that extrapolating those findings to a larger area is not satisfactory.

Climate warming has a serious impact on the avifauna and seriously changes distributions and the migratory status of species. For example, in contrast to descriptions in [53], Eastern Imperial Eagle, Stock Dove, Dunnock, Chiffchaff, European Robin, and Rustic Bunting are now residents in winter and not just summer visitors to this region. Middle Spotted Woodpeckers have also been recorded in Tatarstan, far in the east of the continent. This once again emphasizes how important data collected from little-studied areas (which are under-represented in the world scientific literature) are for a global understanding of events occurring in nature.

Our study is an attempt to show the spatial distribution of birds in winter in Eastern Europe. At this stage of the work, long-term dynamics in the abundance of bird populations and individual species have not been taken into account. There is a need for further research using abundance data to clearly show how the spatial structure of birds is changing under the influence of a changing climate.

We were limited in the elevation gradient, and so there were no species in our study that preferred high-elevation sites. Studies of the effect of elevation (for example, using data east of Tatarstan closer to the Ural Mountains) on bird populations would merit attention. Our research was conducted on big plots using long transects, with basic measures of food resources, and possibly may not reflect the preferences of specific species for microhabitats. It is possible that detectability may vary between early and late winter, for example by increased snowfall, or greater singing activity, although detected numbers were still generally lower in late winter.

5. Conclusions

In conclusion, large-scale as well as long-term monitoring is necessary for the ecological monitoring of the state of forests, to identify changes to the distribution and density of birds (especially rare and endangered species) in the context of current and future climate changes. The year 2023 was the hottest on record for Tatarstan, so the latest research is

most important, coupled with further perturbations in the winter bird population. Data on the occurrence of 17 rare and endangered bird species will be used to supplement the Red Book of the Republic of Tatarstan.

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Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A. Weather Details for the Study Winters

Table A1. Mean Monthly Temperatures (°C) for the Kazan meteorological station †.

	November	December	January	February	March
2018/9	−2.37	−8.07	−10.27	−7.02	−0.82
2019/20	−1.77	−4.08	−2.93	−3.23	2.92
2020/1	−2.33	−4.09	−9.89	−14.69	−4.29
2021/2	−0.39	−10.69	−9.89	−3.14	−4.19
2022/3	−1.64	−8.10	−11.60	−7.60	1.65

† source: https://data.giss.nasa.gov/gistemp/station_data_v4_globe/, accessed on 9 June 2024.

Table A2. Number of days on which snow fell at the Kazan meteorological station ‡.

	November	December	January	February	March
2018/9	8	25	27	25	20
2019/20	7	15	25	22	6
2020/1	14	20	29	19	18
2021/2	19	26	27	21	14
2022/3	18	23	20	27	13

‡ source: <https://en.tutiempo.net/>, accessed on 9 June 2024.

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