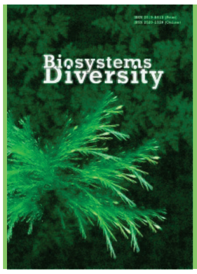

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Global climate change promotes the expansion of rural and synanthropic bird species: The case of Zhytomyr region (Ukraine)

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The article reveals which ecological groups of birds in Zhytomyr region are most vulnerable to global climate change and which birds will benefit from warming in the next 70 years. The following data networks were used as predictors of bird ecological niche: climatic biogeographic variables, soil properties and indicators of landscape cover types. The results of the ENFA analysis were used to derive ecological niche margins for bird species, which were subjected to three principal component analyses to estimate marginality along bioclimatic, edaphic, and landscape variables. The bird species habitat preference index was estimated using the Maxent procedure. The assessment was made on the basis of both current predictors and projected climate variables. It was found that the climatic conditions of the Zhytomyr region are close to the European average. The average annual temperature in Zhytomyr region is 2.1 °C higher than the European average. Furthermore, the average value of monthly temperature ranges, isothermality, annual temperature range and seasonality in Zhytomyr region do not differ significantly from the European average. The maximum temperature of the warmest month in Zhytomyr region is 1.4 °C higher than the European average, while the minimum temperature of the coldest month is 1.7 °C higher. The temperature of the wettest quarter is 4.6 °C above the European average, while the temperature of the driest quarter is 2.3 °C below. The temperatures of the warmest and coldest quarters in Zhytomyr region are slightly higher than the European average (1.8 and 1.6 °C, respectively). The annual precipitation in Zhytomyr region exceeds the European norm by 20 mm. Zhytomyr region exhibits a distinctive pattern of precipitation, with a significantly higher amount of precipitation for the wettest and warmest quarters than the European average. The climate change forecast for the next 70 years indicates that the average annual temperature in Europe can be expected to increase by 4.1°C. For Zhytomyr region, the average annual temperature is likely to increase by 4.4 °C. Furthermore, other temperature indicators are also expected to increase. The contrast of thermal conditions throughout the year will decrease in the future. Precipitation in Europe will increase by 60.3 mm per year on average. In Zhytomyr region, precipitation will increase by 87.2 mm per year compared to the current state. Based on the estimates of the marginality of the birds' ecological niche, principal component analyses of climatic, edaphic and landscape projections were conducted. The principal component analysis of the climatic projection of the ecological niche identified three principal components with eigenvalues exceeding one. Principal component 1 was characterised by a high correlation with temperature bioclimatic variables, which allowed us to interpret this principal component as the position of the species optimum in the thermal gradient. Principal component 2 exhibited a high correlation with bioclimatic variables indicative of precipitation, thereby enabling this principal component to be meaningfully interpreted as the position of the species optimum in the precipitation gradient. Principal component 3 exhibited high correlation coefficients with bioclimatic variables indicative of rainfall variability, thereby enabling this principal component to be interpreted as the position of the species optimum in the rainfall variability gradient. The principal component analysis of the variation of the marginality parameters of the projection of bird ecological niches onto the matrix of diversity of landscape cover types allowed us to extract three principal components with eigenvalues greater than one. Principal component 1 was meaningfully interpreted as the position of the species in the habitat gradient from open spaces (grassland, sparse shrubs, cropland, bare) to forest. This component can also be denoted as the ratio of campophilic/dendrophilic bird species. Principal component 2 denotes the ratio of open space bird species (water, wetland) to birds that prefer built, cropland and trees. This allows us to interpret this principal component as the ratio of wetland (moisture-loving campophilic)/rural bird species. Principal component 3 is positively correlated with the trend of preference for built and water (urbanised areas are usually associated with water bodies) and negatively correlated with trees, shrubs, bare and wetland. This principal component can be interpreted as the position of the species optimum in the urban/rural bird species gradient. It is anticipated that an increase in campophilic bird species compared to dendrophilic species will be the predominant trend in the next 70 years as a response to global climate change. Moisture-loving campophilic species will be outcompeted by rurally-dependent species, and rurally-dependent species will be outcompeted by urban species.

Keywords: Ecological Niche Factor Analysis; Maxent; biogeographic predictors; prediction; climate warming.

Introduction

The phenomenon of global climate change has already resulted in a decline in the number of species and the extinction of species. In the field of modern ecology, the primary conservation priority is to predict and reduce the consequences of climate change and its mutual impact with changes in land use (Jetz et al., 2007). Climate change represents a significant threat to global biodiversity, resulting in alterations to the distribution and abundance of a multitude of taxa (Chen et al., 2011; Stephens et al., 2016). These losses are typically attributed to climate change occurring at a pace that is beyond the capacity of populations to adapt. The extent to which climate change is responsible for the observed shifts in species ranges across vast geographical regions, in comparison to other potential drivers of change, remains a subject of contention (Comte, 2020). Climate change is associated with a shift in species ranges towards higher latitudes and altitudes (Gillings et al., 2015). Although the average rate of range change indicates a significant shift to higher altitudes and latitudes for many taxa, the majority of species are not moving in the expected directions (Rubenstein et al., 2023). The interaction between changes in temperature and precipitation will result in a multidirectional transformation of species ranges (VanDerWal et al., 2013). Climate change is causing shifts in the geographical distribution of species, but populations are also adapting to environmental variation at different rates in different places in their range (Donelson et al., 2019). The interaction of climate change, land-use transformation and human persecution, as well as other site-specific events, can also result in range shifts (Rumpf et al., 2019).

Climate change is altering ecological communities, affecting individual species and the interactions between them. Climate contributes to, but is not the only factor, determining the location of range boundaries for most terrestrial species (Thomas, 2010). The impact of climate change on species ranges has long been predicted (Peters & Darling, 1985) because species distribution is largely dependent on thermal tolerance (Kukal et al., 1991). The rate of climate change is spatially heterogeneous (Loarie et al., 2009), which can cause spatial differences in population responses to climate change among species. In addition, seasonally asynchronous climate change regimes, when certain periods of the year in a region are warming and others are cooling, limit the response of species to climate change more than rapid warming, leading to intraspecific differences in response to climate change and a reduction in local populations (Senner et al., 2018). Nevertheless, the intensity of anthropogenic climate change may exceed the ability of many species to adapt to changing climate tolerance zones (Bedford et al., 2012), which gives reason to expect that climate change will accelerate the rate of species extinction (Maclean & Wilson, 2011). The response of the range, both at the pole and equatorial boundaries of the range, depends on the proximity of the fundamental limits of the thermal niche (Sax et al., 2013). The distribution of wintering birds is the focus of much of the current research on thermal constraints within bird ranges (Zuckerberg et al., 2009), in which thermal release from cold constraints, ie minimum winter temperature, promotes range expansion towards the poles by reducing metabolic demand (Root, 1988). The distribution of breeding birds similarly reflects thermal constraints (Marjakangas et al., 2022). However, direct studies of thermal limits at the breeding range boundary have been rarely conducted (Melles et al., 2011), despite the potential fitness implications arising from loss of or divergence from a thermal niche (Jiguet et al., 2010). The risk of extinction increases if species' climatic niches shift in geographic space (Manes et al., 2021), and species populations are unable to respond similarly, leading to a shrinkage of their geographic ranges (Di Marco et al., 2021). A climate-driven extinction affects populations where warming leads to exceeding the tolerable limits of local temperature conditions expected along equatorial range boundaries (Thomas, 2010). A range expansion due to global warming is expected along the polar range boundaries as a result of optional colonization of new territories where warming has reduced barriers to dispersal and the establishment of new populations (Sunday et al., 2012).

Thus, different processes are likely to determine how species populations respond to climate change, depending on whether populations are located towards the pole or equator edge of their range. Limitations near the range boundaries of a species can be direct if temperatures exceed thresholds that the species can withstand after behavioral thermoregulation is taken into account (Robinson et al., 2007). In addition, the geographic distribution of a species that represents an occupied or exploited niche can be positioned relative to a fundamental niche such that some parts of the distribution are closer to the boundaries of the fundamental niche (Araújo et al., 2013). The expansion of ranges towards the poles is now widely observed among species of many taxa and mostly in the direction expected by climate change (Sunday et al., 2012). While range boundaries at the poles reflect climate-related barriers, failure to track warming along these range boundaries results in a climate debt (Devictor et al., 2012). The extinction of populations as a result of climate change has been observed in terrestrial ecosystems, but it is much less well characterized than range expansion along poleward boundaries (Parmesan & Yohe, 2003). Perhaps the most obvious and particularly long-standing explanation for these observations is that range boundaries toward the poles directly reflect species tolerance to the environment, especially temperature, while range boundaries toward the equator reflect biotic interactions (Cahill et al., 2014).

There are several reasons why species may not exhibit geographic variation in their measured thermal niches, including habitat requirements relative to habitat availability (Coristine & Kerr, 2015), phenotypic variation (Pichancourt & van Klinken, 2012), a niche dynamic or climate specific niche change relative to the species' geographic location (Monahan & Tingley, 2012), dispersal ability (Bedford et al., 2012), compensatory dynamics (Doak & Morris, 2010), and life cycle traits (Tingley et al., 2012). Land-use change and habitat loss can prevent some species from dispersing quickly enough to track geographic shifts in their climatic niches (Sax et al., 2013), leading to climate-induced biotic homogenization as generalists successfully move to new locations while specialists cannot (White & Kerr, 2007). The dynamics of climate conditions, including the interaction of multiple climate variables, may also be accompanied by an increase in the frequency and/or intensity of extreme weather events (VanDerWal et al., 2013). The extreme events may exceed the species' tolerance and cause population extinctions, as well as inhibit or alter the climate responses of the range (i.e., cause extinction of a population that has successfully settled outside the historical range of the species). Adult birds can tolerate temperatures in breeding areas which can often be colder than in wintering areas (Boucher-Lalonde et al., 2014). However, thermoregulatory constraints during the breeding season mean that species should have a lower tolerance for temperatures that approach thermal niche limits (due to gradual climate change or stochastic changes resulting from extreme weather events) during the breeding season (Jankowski et al., 2013). This suggests that for adult birds, thermal limits can vary seasonally (Monahan, 2009) due to physiological changes associated with breeding status (Vehrencamp, 1982), while young birds are highly sensitive to temperature-related mortality due to their lower ability to thermoregulate. Survival rates of young birds decline sharply when temperatures rise, as during extreme heat events, leading to declines in bird populations (Albright et al., 2011), despite the plasticity of adult behaviour in response to warming during nesting (Vedder, 2012). The extent to which species distributions change over geographic and niche space, regardless of such behavioural and phenotypic plasticity, will determine potential management interventions and possibly the prospects for conservation (Coristine & Kerr, 2015).

The assessment of habitat suitability for populations requires a comprehensive analysis aimed at evaluating the suitability of habitats and environmental conditions that support the survival and reproductive success of a species (S. B. Phillips et al., 2006). This comprehensive assessment involves careful consideration of the various factors that collectively define the ecological landscape that supports the species, including climate, nesting habitat, human disturbance, conservation efforts, habitat requirements, and food and water availability. To identify suitable habitat characteristics, a species response model serves as a tool to assess habitat quality and determine the spatial distribution of suitable habitat (Van der Lee et al., 2006). The empirical species response models in a gradient of environmental factors were developed to predict species distribution by correlating species abundance with surrounding habitat characteristics, which provides a differentiated approach to assessing habitat suitability. Among the widely used distribution models, the maximum entropy model (Maxent) stands out due to its unique approach and outstanding performance. In particular, unlike other species distribution models, Maxent incorporates both species distribution data and environmental predictor variables to model suitable habitat (Phillips & Dudík, 2008). Due to its non-parametric flexibility in handling complex species-environment relationships, robustness to overfitting, and overall high predictive performance, as validated by many habitat modelling applications, Maxent has quickly become one of the most widely used tools for species ecological niche modelling (Radosavljevic & Anderson, 2014). For predicting distribution and suitable habitat for species of conservation concern, Maxent is highly effective based on its ability to make accurate and unbiased predictions based on limited presence-only data. To model suitability and identify the environmental factors that have the greatest impact on geographic distribution, Maxent allows you to combine species occurrence records with relevant climatic, topographic, and land cover predictor layers.

The aim of this article is to identify which ecological groups of birds in Zhytomyr region are most vulnerable to global climate change and which birds will benefit from warming in the next 70 years.

Material and methods

The data on the species composition of the avifauna of Zhytomyr region were obtained from Avibase – World Bird Database (https://avibase.bsc-eoc.org). The information on the occurrence of bird species within Europe was derived from the GBIF database (www.gbif.org) using the rgbif library. The following data sets were used as predictors of the ecological niche of birds: climatic biogeographic variables, soil properties, and indicators of landscape cover types. Climate change is a serious danger to the survival of species, which can lead to a shift in geographical ranges. The derivation of bioclimatic factors from monthly temperature and precipitation data provides key variables for modelling species distribution. These include seasonality, environmental extremes, annual trends and temperature/rainfall ranges. Nineteen bioclimatic variables were extracted from the WorldClim data and adapted to the geographical extent of the study area. The data were obtained using the raster library. Projected data on bioclimatic variables were obtained for the next 70 years based on the Coupled Model Intercomparison Project Phase 5 (CMIP5) model (Lynch et al., 2016). Data on the proportions of landscape cover types ("trees", "grassland", "shrubs", "cropland", "built", "bare", "snow", "water", "wetland", "moss") were obtained using the geodata library. The values were obtained from the ESA WorldCover dataset with a resolution of 0.3 seconds (https://esa-worldcover.org/en). Information on soil properties was obtained using the geodata library. Data were obtained from the SoilGRIDS database (Hengl et al., 2017). ENFA (Hirzel et al., 2002) was performed using the adehabitatHS library (Calenge, 2006). The results of the ENFA analysis were used to derive ecological niche margins for bird species, which were subjected to three principal component analyses: for estimates of marginality along bioclimatic, edaphic and landscape variables. The bird species habitat preference index was estimated using the Maxent procedure (Elith et al., 2011; Panchenko, 2022). The assessment was based on both current predictors and projected climate variables (Zimaroeva et al., 2016).

Results

The climatic conditions in Zhytomyr region are close to the European average (Table 1). The average annual temperature in Zhytomyr region is 2.1 °C higher than the European average. The average value of monthly temperature ranges, isothermicity, annual temperature range and seasonality in Zhytomyr region do not differ significantly from the European average. The maximum temperature of the warmest month in Zhytomyr region is 1.4 °C higher than the European average, and the minimum temperature of the coldest month is 1.7 °C higher than the European average. The temperature of the wettest quarter is 4.6 °C above the European average, and the temperature of the driest quarter is 2.3 °C below the European average. The temperatures of the warmest quarter and the coldest quarter in Zhytomyr region are slightly higher than the European average (1.8 and 1.6 °C). The annual rainfall in Zhytomyr region exceeds the European norm by 20 mm. The peculiarity of Zhytomyr region is that the amount of precipitation for the wettest quarter and the warmest quarter is significantly higher than the European average.

Table 1
The descriptive statistics of environmental factors in the current state and the forecast of climate change for the next 70 years

Ecological factor	Europe		Zhytomyr region	
	current state	future state	current state	future state
Average annual temperature, °C (Bio1)	5.15 ± 4.88	9.28 ± 4.40	7.22 ± 0.16	11.58 ± 0.14
Average of monthly temperature ranges, °C (Bio2)	8.49 ± 1.19	6.91 ± 1.83	8.49 ± 0.05	6.66 ± 0.07
Isothermicity, % (Bio3)	2.59 ± 0.58	2.31 ± 0.71	2.51 ± 0.03	2.42 ± 0.04
Seasonality of temperature, standard deviation × 100 (Bio4)	86.74 ± 22.32	82.83 ± 22.17	88.34 ± 0.70	76.39 ± 0.70
Maximum temperature of the warmest month, °C (Bio5)	22.74 ± 4.11	26.22 ± 4.22	24.14 ± 0.18	26.98 ± 0.10
Minimum temperature of the coldest month, °C (Bio6)	–10.65 ± 7.67	–4.14 ± 7.45	–8.92 ± 0.16	0.03 ± 0.14
Annual temperature range, °C (Bio7)	33.39 ± 7.18	30.36 ± 7.28	33.06 ± 0.20	26.95 ± 0.17
Temperature of the wettest quarter, °C (Bio8)	13.43 ± 5.05	16.29 ± 5.86	18.07 ± 0.20	21.46 ± 0.18
Temperature of the driest quarter, °C (Bio9)	–1.28 ± 9.40	5.60 ± 7.96	–3.56 ± 0.18	3.53 ± 1.01
Temperature of the warmest quarter, °C (Bio10)	16.23 ± 3.76	20.00 ± 3.69	18.07 ± 0.20	21.46 ± 0.18
Temperature of the coldest quarter, °C (Bio11)	–6.01 ± 6.99	–1.23 ± 6.59	–4.42 ± 0.15	1.92 ± 0.13
Annual precipitation, mm (Bio12)	620.26 ± 0.34	680.56 ± 0.35	640.06 ± 0.02	727.28 ± 0.02
Precipitation of the wettest month, mm (Bio13)	78.61 ± 0.34	87.59 ± 0.37	95.16 ± 0.03	105.05 ± 0.03
Precipitation of the driest month, mm (Bio14)	29.15 ± 0.56	30.24 ± 0.63	31.19 ± 0.04	33.59 ± 0.05
Seasonality of precipitation (coefficient of variation), % (Bio15)	29.37 ± 8.91	30.25 ± 9.14	37.04 ± 2.16	38.05 ± 1.73
Precipitation for the wettest quarter, mm (Bio16)	214.53 ± 0.35	237.21 ± 0.37	251.58 ± 0.03	287.93 ± 0.03
Precipitation for the driest quarter, mm (Bio17)	98.91 ± 0.48	105.06 ± 0.52	101.57 ± 0.04	111.62 ± 0.04
Precipitation for the warmest quarter, mm (Bio18)	185.38 ± 0.5	200.22 ± 0.64	251.58 ± 0.03	287.93 ± 0.03
Precipitation of the coldest quarter, mm (Bio19)	126.98 ± 0.51	149.62 ± 0.46	112.84 ± 0.04	125.07 ± 0.05
Density of organic carbon, kg/m^3 (OCD)	5.33 ± 0.23	5.33 ± 0.23	4.03 ± 0.04	4.03 ± 0.04
Clay (<0.002 mm), % (Clay)	18.00 ± 0.68	18.00 ± 0.68	16.75 ± 0.27	16.75 ± 0.27
Silt (0.002-0.05 mm), % (Silt)	36.18 ± 0.25	36.18 ± 0.25	40.73 ± 0.24	40.73 ± 0.24
Sand (> 0.05 mm), % (Sand)	39.85 ± 0.49	39.85 ± 0.49	39.78 ± 0.32	39.78 ± 0.32
Total nitrogen, g kg-1 (N)	7.98 ± 0.42	7.98 ± 0.42	9.95 ± 0.14	9.95 ± 0.14
Coarse fragments (> 2 mm), % (CF)	10.65 ± 0.32	10.65 ± 0.32	7.61 ± 0.18	7.61 ± 0.18
Soil density, g/cm^3 (BD)	0.88 ± 0.17	0.88 ± 0.17	1.08 ± 0.03	1.08 ± 0.03
Soil acidity (pH)	5.68 ± 0.14	5.68 ± 0.14	6.18 ± 0.05	6.18 ± 0.05
Proportion of trees in the landscape cover (Trees)	0.45 ± 0.31	0.45 ± 0.31	0.43 ± 0.18	0.43 ± 0.18
Proportion of grasses in the landscape cover (Grassland)	0.21 ± 0.16	0.21 ± 0.16	0.19 ± 0.08	0.19 ± 0.08
Proportion of shrubs in the landscape cover (Shrubs)	0.01 ± 0.03	0.01 ± 0.03	0.02 ± 0.08	0.02 ± 0.08
Proportion of agricultural land in the landscape cover (Cropland)	0.17 ± 0.22	0.17 ± 0.22	0.30 ± 0.19	0.30 ± 0.19
Proportion of buildings in the landscape cover (Built)	0.01 ± 0.03	0.01 ± 0.03	0.01 ± 0.01	0.01 ± 0.01
The proportion of plants in the landscape cover (Bare)	0.01 ± 0.02	0.01 ± 0.02	0.01 ± 0.02	0.01 ± 0.02
Proportion of water bodies in the landscape cover (Water)	0.04 ± 0.11	0.04 ± 0.11	0.01 ± 0.01	0.01 ± 0.01
Proportion of marshes in the landscape cover (Wetland)	0.03 ± 0.07	0.03 ± 0.07	0.01 ± 0.02	0.01 ± 0.02

The climate change forecast for the next 70 years indicates that the average annual temperature in Europe is expected to increase by 4.1 °C. For Zhytomyr region, the average annual temperature is likely to increase by 4.4 °C. Other temperature indicators will also increase. The contrast of thermal conditions throughout the year will decrease in the future. Precipitation in Europe will increase by 60.3 mm per year on average. In Zhytomyr region, precipitation will increase by 87.2 mm per year compared to the current state. The habitat preference index (HSI) of Zhytomyr region's avifauna under current conditions varies from 0.002 to 0.570 (median is 0.102, mean ± st. deviation is 0.132 ± 0.011, Fig. 1). The HSI for 223 species (85.1%) is less than 0.25, the HSI for 36 species (13.7%) is in the range of 0.25–0.50, and the HSI for 3 species (1.1%) is greater than 0.50. The group of species for which the conditions in the Zhytomyr region are closest to optimal includes *Clanga clanga* (Pallas, 1811), *C. pomarina* (C. L. Brehm, 1831) and *Ciconia nigra* (Linnaeus, 1758). The climate change forecast suggests that in 70 years, the HSI will range from 0.001 to 0.647 (median is 0.079, mean ± st. deviation is 0.102 ± 0.097). The sign test indicates a statistically significant difference between the HSI under current conditions and the projected HSI in 70 years ($Z = 4.0$, $P < 0.001$). HSI for 242 species (92.4%) will be less than 0.25, HSI for 18 species (6.9%) will be in the range of 0.25–0.50 and HSI for 2 species (0.8%) will be greater than 0.50. For the species *C. clanga* and *C. pomarina*, the ecological conditions will remain close to optimal. For 159 species (60.1%), the HSI will decrease by more than 0.01 over the next 70 years. For 20 species (7.6%), the HSI will remain virtually unchanged (changes will be in the range of –0.01 to +0.01). For 83 species (31.7%), the HSI will increase by more than 0.01 over the next 70 years.

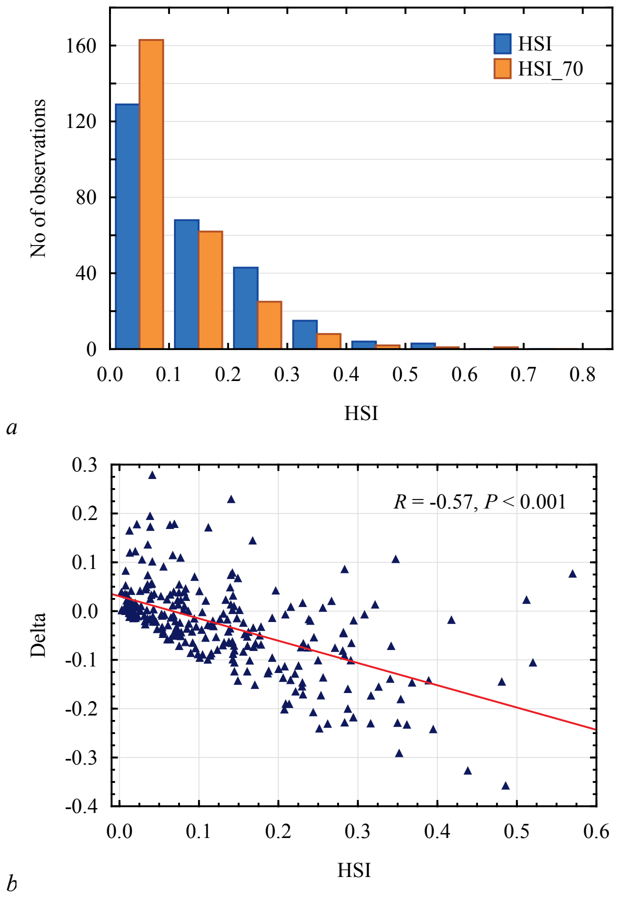

Fig. 1. Histograms of the distribution of habitat suitability indices (HSI) under current conditions and under the projection of global climate change in 70 years (*a*) and scatter plot of HSI values under current conditions and its change (Delta) under the projection of global climate change in 70 years (*b*): the abscissa is provided: HSI under current conditions (blue) and projected global climate change in 70 years (orange) (*a*) and HSI under current conditions (*b*); the ordinate is the number of bird species (*a*) and the change in HSI projected in 70 years compared to the current state (Delta)

Principal component analyses of the climatic, edaphic and landscape projections were conducted based on the estimates of the marginality of the bird ecological niche. The principal component analysis of the climatic projection of the ecological niche allowed us to identify three principal components with eigenvalues exceeding one (Table 2). Principal component 1 was characterised by a high correlation with temperature bioclimatic variables, which allowed us to interpret this principal component as the position of the species optimum in the thermal gradient. Principal component 2 had a high correlation with bioclimatic variables indicating the amount of precipitation, which allowed this principal component to be meaningfully interpreted as the position of the species optimum in the precipitation gradient. Principal component 3 had high correlation coefficients with bioclimatic variables indicating rainfall variability, and this principal component was interpreted as the position of the species optimum in the rainfall variability gradient.

Table 2
Principal component analysis of the variation of marginality parameters of the climatic projection of bird ecological niches (only statistically significant correlation coefficients for $P < 0.05$ are shown)

Bioclimatic variable	Climate 1 $\lambda = 8.8$, 46.6%	Climate 2 $\lambda = 7.8$, 40.9%	Climate 3 $\lambda = 1.4$, 7.8%
Bio1	0.98	–	0.18
Bio2	0.52	0.70	–
Bio3	0.94	–0.29	–
Bio4	–0.74	0.65	–
Bio5	0.78	0.57	0.15
Bio6	0.95	–0.28	0.15
Bio7	–0.64	0.74	–
Bio8	–0.18	0.79	0.45
Bio9	0.99	–0.12	–
Bio10	0.83	0.48	0.19
Bio11	0.96	–0.22	0.13
Bio12	–	–0.98	–
Bio13	–	–0.85	–0.39
Bio14	–0.55	–0.73	0.38
Bio15	0.17	0.65	–0.72
Bio16	–	–0.91	–0.29
Bio17	–0.33	–0.86	0.35
Bio18	–0.88	–0.38	0.23
Bio19	0.65	–0.74	–0.15

The principal component analysis of the variation of marginality parameters of the edaphic projection of bird ecological niches resulted in the extraction of two principal components with eigenvalues exceeding one (Table 3). The structure of correlations with edaphic variables allowed us to interpret principal component 1 as the position of the species optimum in the gradient of soil nutrient content, and principal component 2 as the position of the species optimum in the gradient of soil aggregate structure.

Table 3
Principal component analysis of the variation of marginality parameters of the edaphic projection of bird ecological niches (only statistically significant correlation coefficients for $P < 0.05$ are shown)

Variable	Edaphic 1 $\lambda = 6.1$, 76.3%	Edaphic 2 $\lambda = 1.1$, 13.8%
Organic carbon density	0.96	0.13
Clay (< 0.002 mm) in fine earth	–0.96	–0.16
Silt (0.002–0.05 mm) in fine earth	–0.75	0.24
Sand (> 0.05 mm) in fine earth	0.97	–
Total nitrogen	0.92	–0.16
Vol. fraction of coarse fragments (> 2 mm)	–0.15	0.98
Bulk density of the fine earth fraction	–0.97	–
pH	–0.98	–

The principal component analysis of the variation in the marginality parameters of the projection of bird ecological niches onto the matrix of diversity of landscape cover types allowed us to extract three principal components with eigenvalues greater than one (Table 4). Principal component 1 was meaningfully interpreted as the position of the species in the habitat gradient from open spaces (Grassland, Sparse Shrubs, Cropland, Bare) to forest. This component can also be denoted as the ratio of Campophilic/Dendrophilic bird species. Principal component 2 denotes the ratio of open space bird species (Water, Wetland) to birds that prefer Built, Cropland and Trees. This allows us to interpret this principal component as the ratio of Wetland (moisture-loving Campophilic)/Rural bird species. Principal component 3 is positively correlated with the trend of preference for Built and Water (urbanised areas are usually associated with water bodies) and negatively correlated with Trees, Shrubs, Bare and Wetland.

This principal component can be interpreted as the position of the species optimum in the Urban/Rural bird species gradient.

Table 4
Principal component analysis of the variation of marginality parameters of the projection of bird ecological niches onto the matrix of diversity of landscape cover types (only statistically significant correlation coefficients for $P < 0.05$ are shown)

Land cover type	Campophilic/ Dendrophilic $\lambda = 3.5$, 43.6%	Wetland/Rural $\lambda = 1.6$, 19.5%	Urban/Rural $\lambda = 1.1$, 14.1%
Trees	–0.93	–0.16	–0.27
Grassland	0.77	–	–
Shrubs	0.76	–	–0.42
Cropland	0.72	–0.25	–
Built	0.29	–0.57	0.67
Bare	0.88	–	–0.21
Water	–	0.71	0.59
Wetland	0.26	0.80	–0.14

Variations in HSI as a result of global climate change over the next 70 years will depend on the preference of bird species for climatic conditions (Fig. 2). In the future, HSI will increase in species that are more thermophilic and prefer conditions with higher precipitation. The factor of precipitation variability will not be significant in changes in habitat conditions for birds in Zhytomyr region. Habitat conditions will improve for bird species that are able to survive in habitats with poor soils (Fig. 3). Another positive factor will be adaptation to conditions in habitats with more structured soils. An increase in campophilous bird species compared to dendrophilous species will be the predominant trend in the next 70 years as a response to global climate change (Fig. 4). In addition, humid campophilous species will lose ground to rurally-dependent species, and rurally-dependent species will lose ground to urban species.

Discussion

Global climate change will lead to shifts in the existence of living organisms in the near future. Climate change is causing ecosystems to become unbalanced through changes in temperature and precipitation (Reyes-García et al., 2016). Such climate change affects the distribution and availability of critical resources for wildlife, such as food, water and shelter (Godde et al., 2021). Species respond to climate change through changes in morphology and behaviour, phenology and shifts in geographic range (Weiskopf et al., 2020).

Habitat conditions will become worse for about two-thirds of bird species within Zhytomyr region within 70 years. For a small number of birds, habitat conditions will not change. However, it can be assumed that in addition to the impact on the species composition of communities, the number of birds will be significantly affected. Certain habitats become uninhabitable as temperatures rise, forcing species to migrate in search of favourable conditions (Ekman et al., 2024). This leads to range shifts, with species moving to higher latitudes or higher altitudes. However, not all species can adapt or migrate quickly enough, leading to population declines and local extinctions. It should also be noted that climate change will be out of sync with changes in other components of the ecosystem, so that species for which climatic conditions become favourable may not be able to find locations with other favourable conditions, as characterised by the parameters of ecosystem productivity and landscape diversity. Species that are currently in the most favourable climatic and other environmental conditions will suffer the greatest decline. Usually, such species are dominant in terms of numbers in communities or demonstrate the stability of occurrences in communities. Climate change will adversely affect species that are currently dominant, which will negatively affect the overall number of bird communities. In turn, species that are currently on the periphery of their climatic range will see a significant improvement in climatic conditions. However, if the improvement in climatic conditions is not accompanied by other changes in the environment, which is unlikely, then there will be no response in the form of a compensatory increase in the number of communities.

Our results indicate that the role of temperature in determining the ecological niche within the ranges of bird species is more important than precipitation and climate variability (continentality), as evidenced by the predominant loadings of temperature bioclimatic predictors on principal component 1. Our results are in line with generalisations that the northern limit of a species' range is more influenced by abiotic factors such as low temperatures, while the southern limit is determined by climatic factors such as heat or water shortages in arid regions and biotic factors in more humid regions (Böhning-Gaese & Lemoine, 2004). The bird species of the regional avifauna form a sequence from warm- to cold-tolerant species.

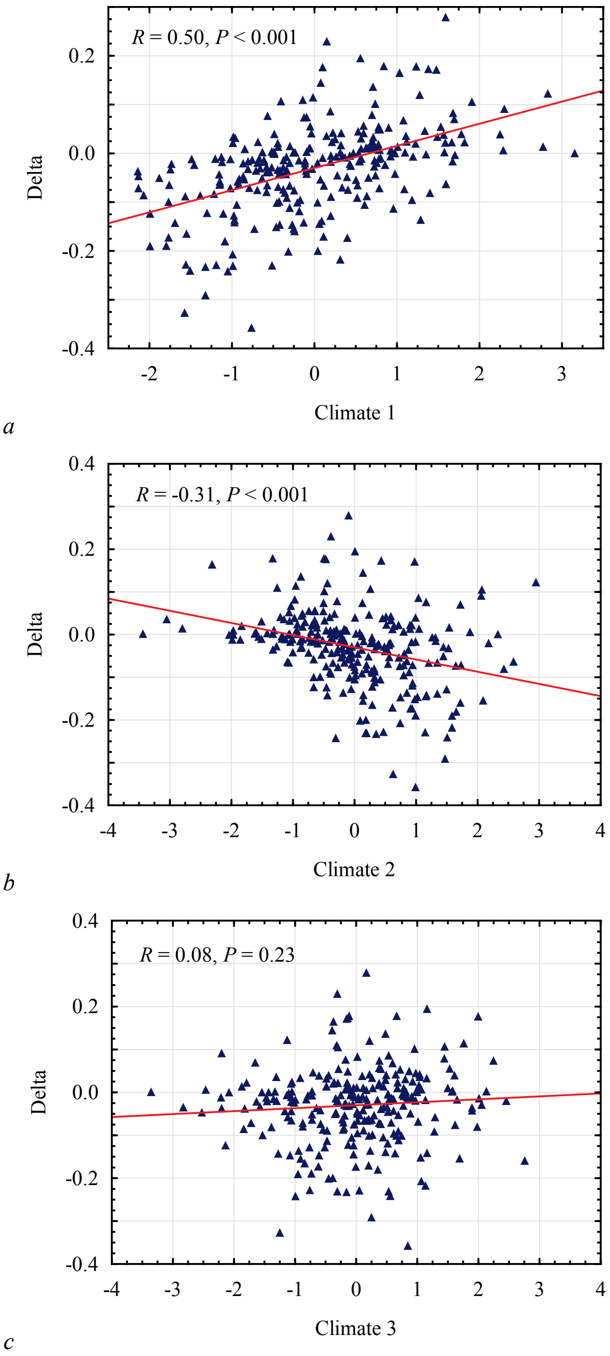

Fig. 2. Dependence of the predicted change in the habitat preference index (HSI) due to global climate change in the next 70 years (ordinate axis, Delta) and the marginality parameters of the climate projection of bird ecological niches: abscissa: *a* is the position of the species' optimum in the thermal gradient (principal component Climate 1), *b* is the position of the species' optimum in the precipitation gradient (principal component Climate 2), and *c* is the position of the species' optimum in the precipitation variability gradient (principal component Climate 3)

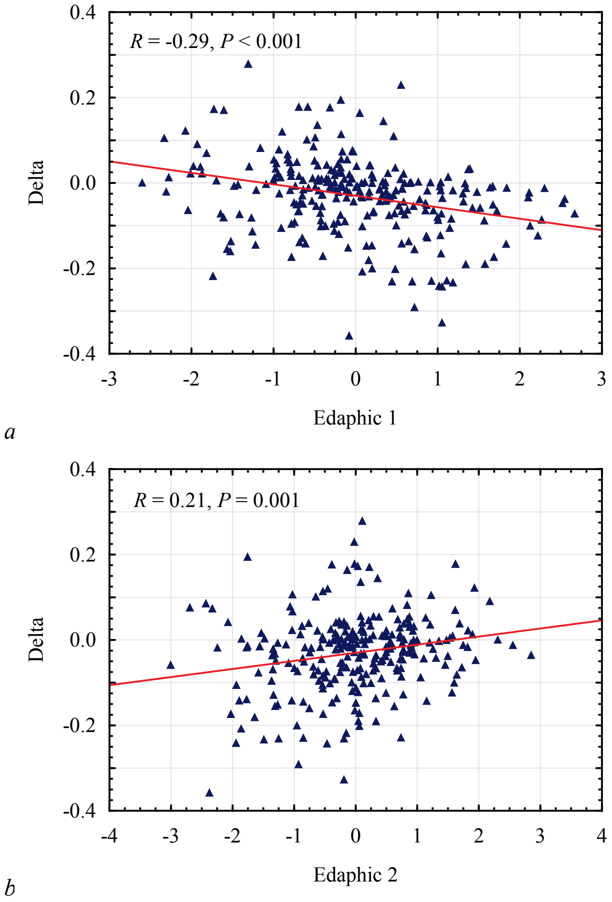

Fig. 3. Dependence of the predicted change in the habitat preference index due to global climate change in the next 70 years (ordinate axis, Delta) and the marginality parameters of the edaphic projection of bird ecological niches: abscissa: *a* is the position of the species' optimum in the gradient of soil nutrient content (Edaphic principal component 1), *b* is the position of the species' optimum in the gradient of soil aggregate structure (Edaphic principal component 2)

The increase in the HIS score suggests that climate warming will lead to an improvement in the climatic regime for warmth-loving species, while the conditions for cold-tolerant species will become worse. It should be noted that the thermal factor has its own structure, which is associated with certain correlations between bioclimatic variables, and the average annual temperature is one of them and does not fully characterise the impact of a complex environmental factor. The thermal factor implies the ordering of species along a gradient, which is marked by a change in the average annual temperature and a decrease in temperature seasonality, annual temperature range, and precipitation during the driest period. Changes not only in the absolute values of bioclimatic variables, but also in the nature of their coordinated dynamics will be reflected in the nature of the impact of this factor on bird species and their communities. That is, an increase in temperatures may have a negative impact on cold-tolerant species, but may not have a positive impact on heat-loving species if it is not accompanied by temperature variability and changes in precipitation patterns. In general, global climate change affects not only the general trend of temperature increase, but is also associated with an increase in the likelihood of extreme weather events and deviations from the usual patterns of climate processes throughout the year. It should be noted that the synchronisation and correlation of weather events is the least predictable aspect of global climate change (Shivanna, 2022).

The importance of edaphic factors should be considered in the context of expanding the interpretation of landscape diversity indicators, as landscape cover types correlate with edaphic indicators (Zhukov et al., 2022). For example, the marginality of ecological niches in the gradient of soil organic matter and nutrients is negatively correlated with the gradient set by the ratio of campophilous to dendrophilous bird species. Edaphic properties are conservative with respect to climate impacts, and some of them will not change significantly as a result of global climate change (Certini & Scalenghe, 2023). This mainly concerns the properties inherited by the soil from the bedrock, namely the particle size distribution of the soil (Zymaroieva et al., 2021). Other indicators, such as chemical composition and organic matter content, can change under climate, but these changes can be moderated by the buffering properties of the soil (Zymaroieva et al., 2019). Predicting the dynamics of changes in soil properties induced by global warming is a separate task (Cornu et al., 2023). In general, soil properties should be considered as a factor in the sustainability of terrestrial ecosystems. Changes in the structure of land cover also have a significant level of conservatism. It can be assumed that the role of anthropogenic changes will be very significant in land cover transformation, but they are more difficult to predict than natural processes, as anthropogenic dynamics are influenced by a number of reasons that are almost impossible to predict.

Climate change and urbanisation are among the most widespread and rapidly increasing threats to biodiversity worldwide (Avtaeva et al., 2021; Langraf et al., 2024a, 2024b). Intensive forest management and high greenhouse gas emissions scenarios could lead to further declines in the number and diversity of forest ecosystem communities (Ekman et al., 2024). Our analysis does not include projections of changes in land cover, but species dependencies on climatic factors can provide insight into projected changes in landscape bird communities, as they differ in their bioclimatic preferences. Therefore, information on projected climate change provides the basis for forecasts of changes in landscape bird communities (Zhukov et al., 2017). Our results indicate a significant correlation between global warming and trends associated with the transformation of natural communities into rural ones, and rural into urbanised communities. Our results are in line with generalisations that rural communities are being transformed by global climate change (Lugo-Morin, 2016). Temperature rise has been recognised as a pronounced consequence of both urbanisation (through the urban heat island effect) and climate change (Sumasgutner et al., 2023). Urban environments are known to form heat islands that model trends that can be expected due to climate change in the environment as a whole. These include an increase in temperature and precipitation. Such changes are already typical of urban environments (Mushtaha et al., 2021). Urban environments are characterised by higher temperatures and more precipitation (Yakovenko & Zhukov, 2021). It is natural that species that are adapted to living in urban environments will gain advantages for living in the natural environment transformed by global climate change. The urban heat island effect is associated with lower species richness and lower functional diversity of birds in cities compared to suburban areas during both the breeding and non-breeding seasons, prompting birds to avoid urban areas or move to cooler suburban areas during both the breeding and non-breeding seasons (Cai et al., 2023). Consideration of the ecological mechanisms that mediate species responses to urbanisation and rising temperatures is a prerequisite for understanding trends in bird communities under global climate change (Sumasgutner et al., 2023).

Urban habitats and landscapes are markedly different from natural habitats outside the city (Koshelev et al., 2021). The main difference lies in the transformation of the territory – from natural green areas to anthropogenic structures and impermeable surfaces (Isaksson, 2018). The importance of urban parks and green spaces for supporting the biodiversity of urban bird communities is noted (Park & Mo, 2021). The favourable impact of not only climate change on the urbanised fraction of the avifauna, but also the spread of urban areas due to both the expansion of large cities and the spread of small towns and villages cannot be ruled out. Some species thrive in the city. These urban species often show pronounced phenotypic differences in behaviour, physiology and morphology from their rural counterparts (Yorkina et al., 2022). These phenotypic changes are associated with specific urban selective factors such as air pollution, artificial lighting at night, noise, different food types, different predation pressure, and human interference (Isaksson, 2018). Climatic conditions can also be expected to become favourable for the spread of synanthropic avifauna into natural habitats, as well as for the expansion of the list of synanthropic species due to adventive species and autochthonous species that have switched to the synanthropic mode. If there is a trend of homogenisation of urban flora and fauna, then as a result of global climate change, we can predict homogenisation of natural communities. Synanthropic fauna will be able to spread into natural habitats, some natural species will become synanthropic, and many natural species will either disappear or become quite rare.

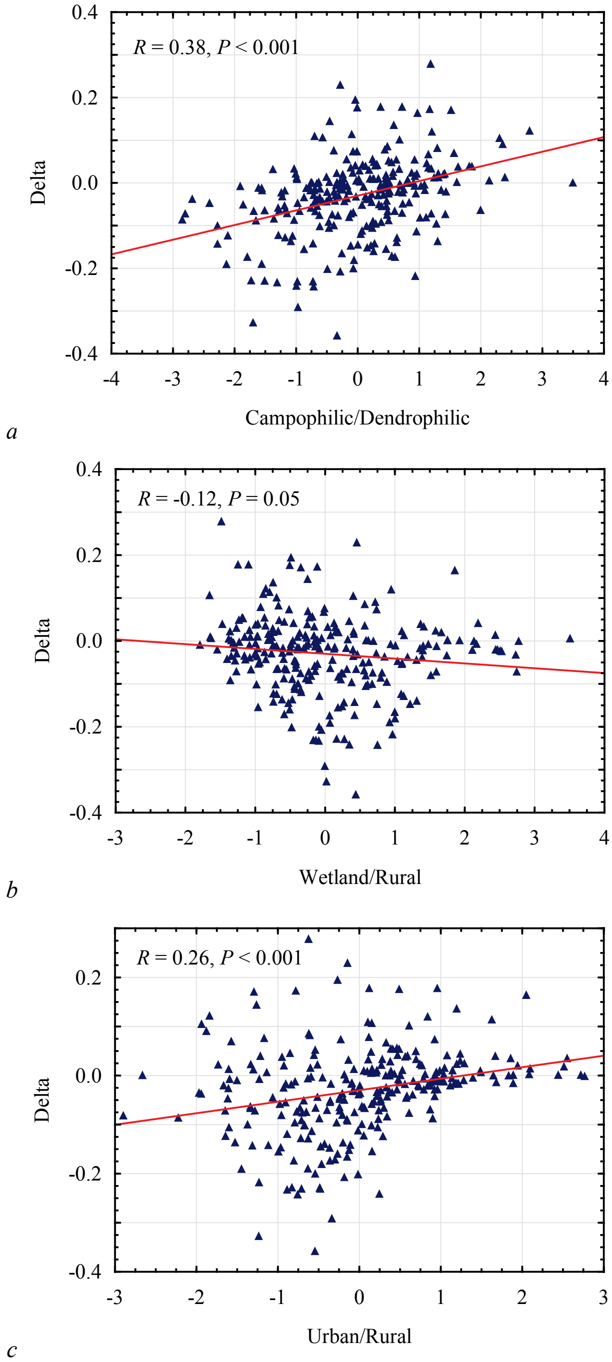

Fig. 4. Dependence of the predicted change in the habitat suitability index due to global climate change in the next 70 years (ordinate axis, Delta) and marginality parameters of the projection of bird ecological niches onto the matrix of diversity of land cover types: abscissa: *a* is the Campophilic/Dendrophilic ecological niche gradient (principal component Campophilic/ Dendrophilic), *b* is the Wetland/Rural ecological niche gradient (principal component Wetland/Rural), and *c* is the Urban/Rural ecological niche gradient (principal component Urban/Rural)

Forecasts for forest bird species typical of the region are not encouraging in the context of global climate change. Open space birds will have an advantage over forest species. The populations of the rare forest bird species *Dendrocopos leucotos* (Bechstein, 1803), which is listed in the Red Data Book of Ukraine, will be very negatively affected. In Polissia, it is more likely to inhabit moist forests or forest floodplains and lakeshores. It is believed that the change in the number of this species is caused by the practice of clear-cutting of old forests. Our results point to the role of climate change in reducing the level of favourable conditions for this species. A reduction in forest cover due to both economic activity and fire risks cannot be ruled out, as an increase in average annual temperature of more than 4 °C will significantly contribute to this. Precipitation will increase, but evaporation will also increase due to higher temperatures, so there will be a significant risk of marshland drainage and burning. Similarly to the steppe zone, it can be assumed that forests will remain in floodplains and the first floodplain terraces of river valleys. In this context, the conservation of forest communities and factors that guarantee the sustainability of the hydrological regime of landscape complexes is an important tool for preventive actions to reduce the negative impact on biodiversity of avifauna of global climate change.

In addition to forest species, wetland birds face significant risks of extinction and reduction of suitable habitats. These are grassland, marsh and waterbird species. Climate change will lead to their displacement in favour of birds adapted to existence in rural habitats. The blackbird (*Turdus merula* Linnaeus, 1758) shows a tendency to settle in rural and urban habitats. The blackbird is one of the most common birds inhabiting forests, agricultural lands and suburban habitats (Chamberlain et al., 1999). Due to global climate change, we can predict an increase in the level of favourable habitat conditions for this species. Our assumptions are in line with findings that agricultural land supports many bird species whose ancestral habitats were deciduous forests that have been replaced by agricultural land (Hatchwell et al., 1996). Forest fragments on agricultural land still support a disproportionate number of breeding birds (Sam et al., 2014), making their conservation an important conservation issue (Deconchat et al., 2009). Several studies have shown that under current climatic conditions, agricultural land is a suboptimal habitat for species originating from forests (Krebs, 1971). Climate change could significantly change the conditions in favour of riparian species. Rural conditions are a combination of low-rise buildings, shrubs, trees and open spaces. Of course, such landscapes are not typically characterised by high population and industrial densities. In turn, climate change will lead to the displacement of rural in favour of urbanised species.

Urbanisation is considered a major driver of biodiversity loss, biotic and seasonal homogenisation (McKinney, 2006). Two main hypotheses describe the response of bird communities to urbanisation: the intermediate disturbance hypothesis and the ecosystem stress gradient hypothesis (McCloy et al., 2022). Both of these hypotheses provide insights into how bird communities respond to urbanisation in terms of diversity and richness and can help predict their resilience and adaptive capacity (Zhukov et al., 2023). According to the intermediate disturbance hypothesis, communities are expected to be more functionally diverse and species-specific when disturbances are at an intermediate level – neither too rare nor too common (Connell, 1978). This hypothesis is usually productive on a temporal scale, but in the context of urbanisation it is often considered on a spatial scale, with intermediate urbanisation conditions, such as peri-urban habitats, urban habitats with green spaces, etc., predicted to be more diverse and therefore more resilient than low or high urbanisation conditions. In contrast to the intermediate disturbance hypothesis, the ecosystem stress gradient hypothesis predicts that resilience, as measured by species richness and/or functional diversity, decreases with increasing habitat stress (Bertness & Callaway, 1994). In the context of urbanisation, this hypothesis predicts that community richness and diversity will be highest in non-urban, undisturbed habitats and lowest in urban habitats (Evans et al., 2018). Empirical evidence suggests a steady decline in diversity and resilience with increasing urbanisation, supporting the hypothesis of an ecosystem stress gradient (McKinney, 2008). There is also evidence for the intermediate disturbance hypothesis. This is evidenced by the observation that species richness of bird communities is often highest at intermediate levels of urbanisation (Lepczyk et al., 2008). In the early stages of urbanisation, when cities are small and the distance from the city centre to natural habitats is short, bird species richness increases (Christie & Hochuli, 2009). This pattern may be explained by the fact that some species prefer the rural habitats (Sisk & Battin, 2002). However, such increases are temporary, and as urbanisation continues, species richness in communities typically decreases (Jokimäki 1993). The available evidence suggests that species richness patterns may be consistent with the intermediate disturbance hypothesis, while diversity patterns are most closely associated with the ecosystem stress gradient hypothesis (McCloy et al., 2022). Our data show that the impact of urbanisation is modulated by the influence of climatic regimes. Therefore, the overall trends in the impact of urbanisation on community biodiversity depend on climatic conditions (Shupranova et al., 2019; Makaida et al., 2021). Climate warming contributes to improved conditions that are favourable for synanthropic bird species. Synanthropic species are either neutral to climate change or show a tendency to improve their status in climatic conditions arising from global warming.

Conclusion

The average annual temperature in Europe is expected to increase by 4.1 °C over the next 70 years, while in Zhytomyr region, the average annual temperature is likely to increase by 4.4 °C. The amount of precipitation in Europe is expected to increase by an average of 60.3 mm per year, with Zhytomyr region experiencing an even greater increase of 87.2 mm per year compared to the current state. In the next 70 years, global climate change will result in a decrease in the habitat preference index for 159 species (60.1%), no change in the index for 20 species (7.6%), and an improvement in habitat conditions for 83 species (31.7%). The differentiation of bird ecological niches by climate regimes is primarily influenced by three main factors: the thermal gradient, precipitation gradient and temporal variability of precipitation throughout the year. In terms of the landscape, bird species can be differentiated according to their Campophilic/Dendrophilic, Wetland/Rural, and Urban/Rural characteristics. Soil conditions further refine the landscape differentiation of bird ecological niches. As a result of global climate change, the habitat preference index will increase for species that are more thermophilic and prefer conditions with higher rainfall. The next 70 years will see an increase in the number of Campophilic bird species compared to Dendrophilic species as a result of global climate change. Moisture-loving Campophilic will be outcompeted by rurally-dependent species, and rurally-dependent species will be outcompeted by urban species.

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